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Long-term changes in composition and distribution patterns in the Iberian herpetofaunal communities since the latest Pleistocene

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ABSTRACT

The climate has undergone significant changes since the end of the Last Glacial Maximum and in the course of the Holocene, parallel to important cultural transformations and migrations in the human communities. The faunal record has also suffered the effects of climate change. Amphibians and reptiles in particular have been shown to be highly sensitive because they are very susceptible to temperature alterations due to their ectothermy. This research presents the first approach to the Iberian paleobiogeography of the different species of amphibians and reptiles from the Late Pleistocene (MIS3) to present times, based on a comparative synthesis of the latest research published in recent years and the fossil record of the 58 archaeo-paleontological sites with significant assemblages. The paleoherpetofaunal associations make it possible to establish two major biotic regions during the Late Pleistocene. The first biotic region was located in the center and south of the Iberian Peninsula, with thermophilic species as the most representative taxa. The second biotic region was formed by the Atlantic-Cantabrian facade and the northeast Iberian area, dominated by hygrophilous and Euro-Siberian species, with an absence of Mediterranean species. After the Last Glacial Maximum there was an unprecedented concurrence in the northern Iberian Peninsula of autochthonous taxa from that area with thermophilic species. In the early Holocene, new species with no previous record in the Iberian Peninsula entered northern Iberia from eastern Mediterranean *refugia*. Finally, the introduction of North African species was the last significant biogeographical change during the Middle-Late Holocene.

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1. Introduction

The last 60,000 years of the Quaternary have been characterized in Western Europe by major climatic and environmental changes as a result of the occurrence of the last great glacial pulsation and the beginning of the current warm interglacial. This time interval begins in MIS 3 (ca. 60,000 to 26,900 B.P.), alternating between phases of warming and cooling climate that correspond to the decline or increase of forests and semi-desert environments until the onset of MIS 2 (26,900 to 14,900 B.P.). At this point there occurs a major cooling process and a remarkable expansion of open arid spaces, with vegetation typical of cold and dry environments and with forest limited to areas of refuge (Fletcher and Sánchez-Goñi, 2008; Fletcher et al., 2010). MIS 1 (which starts at 14,900 B.P.) is characterized by a generalized warming of the climate, especially from the Holocene onwards (11,700 B.P.), and by a rapid increase in wooded areas. However, this phase also presents significant climatic fluctuations, though without outweighing the warm overall dynamic (Fletcher & Sánchez-Goñi, 2008; Fletcher et al., 2009; Walker et al., 2012; Naughton et al., 2015).

These large climatic and environmental changes have had a decisive impact on wildlife. The herpetofauna, reptiles and amphibians, is one of the animal groups that is most sensitive to temperature fluctuations due to the characteristic ectothermy of such organisms (Pough, 1980). This makes it a group of special interest for studying the effects that Quaternary climate changes have had on biodiversity (Araújo et al., 2008). All species of reptiles and amphibians in the Iberian fossil record of the Late Quaternary are currently represented in the Iberian Peninsula (Rage and Roček, 2002; Blain et al., 2011, 2014a, 2016). This facilitates actualist studies that allow us to observe the movements that have occurred

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in the geographical distribution of these groups leading to the current situation and to infer the possible paleoenvironmental and bioclimatic changes at a regional level (Blain, 2009).

To date, 51 species of reptiles and 28 species of amphibians have been described on the Iberian mainland, a herpetofaunal assemblage characterized by a great variability of thermal and ecological requirements (Masó and Pijoan, 2011). This includes typically Mediterranean taxa such as *Acanthodactylus erythrurus*, *Hemidactylus turcicus*, *Hemorrhois hippocrepis*, *Chamaeleo chamaeleon* and *Blanus cinereus*, and other species associated with Euro-Siberian climates such as *Lacerta agilis*, *Zootoca vivipara*, *Mesotriton* (*Ichthyosaura*) *alpestris* and *Rana temporaria*. The widespread mountainous terrain of the Iberian Peninsula has facilitated the emergence of species whose distribution is associated with high mountain climates, especially in northern Spain, examples being *Calotriton asper* and the genus *Iberolacerta* (Carretero et al., 2014). The high degree of knowledge currently available of the 79 herpetofaunal species with a current distribution in the Iberian Peninsula (Pleguezuelos et al., 2002; Masó and Pijoan, 2011; Salvador and Pleguezuelos, 2013; Carretero et al., 2014) results in a good bibliographical, biogeographical and statistical base for an analysis of the Iberian fossil herpetofauna. The biological requirements of each of these species generate particular restrictions that limit their biogeographical distribution and the viability of their populations, both at present and during the Quaternary, allowing us to infer the paleoclimate and the paleobiogeography by means of the fossil record (Blain et al., 2009a).

The phylogenies of different European species suggest the existence of a climatic refuge in the Iberian Peninsula through the successive glacial stages, from which these species would have subsequently repopulated the rest of the continent during the interglacial phases. This is a role similar to that played by the other peninsulas of southern Europe, the Balkans and Italy (Hewitt, 1996, 2000), made possible by the special climatic characteristics of their geographical location (Fletcher et al., 2010; Harrison and Sánchez-Goñi, 2010). In addition, the highly variable Iberian orography allowed the existence of a multitude of areas with different climatic and environmental characteristics, permitting the survival of species more adapted to temperate climates, in contrast to the situation in the rest of the continent (Nieto, 2011).

In the present study, by means of a comparative statistical analysis of the herpetofaunal associations from a total of 118 levels of 38 Iberian archaeo-paleontological sites in the Iberian Peninsula from the last 60,000 years (Fig. 1), we intend to identify the main changes in the distribution, composition and diversity of the reptiles and amphibians during the time interval analyzed. Our aim is to determine the main biogeographical movements of the different herpetofaunal species throughout the Iberian Peninsula and the role of the peninsula as a climate refuge during the Last Glacial Maximum and as a starting point for the subsequent recolonization of northern areas.

2. Material and methods

2.1. Data matrix

First, a bibliographical search has been carried out in the major journals of archaeology, paleontology and zooarchaeology, as well as a search through the major Internet search engines (mainly Google, Yahoo and Bing). For our statistical studies, the taxa identified in 118 levels of 38 paleo-archaeological sites chronologically dated to between early MIS 3 (*ca*. 60,000 B.P.) and the Bronze Age (*ca*. 3500 B.P.) have been compiled. These were then separated into three data matrices on the basis of biogeographical factors (Appendix A, B & C). For each level all the species present in the herpetological record have been included. In the case of genera with a single Iberian species (e.g., genus *Pelobates*), either currently or in the Quaternary fossil record (genus *Testudo*) (Morales and Sanchis, 2009), these have been assigned to the only species in question. The same goes for taxonomic identifications assigned to families that only have a single species present in the Iberian Peninsula (Geoemydidae or Emydidae). However, we have not included the genus-level citations of genera that have two or more species present in the Iberian Peninsula (e.g., genera *Bufo* sensu lato and *Natrix*).

In addition, we have applied some corrections to the data matrix to reduce dispersion and facilitate interpretation. The genus-level citations of the genera *Hyla*, *Lacerta* and *Vipera* from levels in the northern area have been included because of their biogeographical significance. For the same reason, the genus-level citations of *Pelodytes* and *Alytes* have also been included, despite the lack of species-level identification in some cases (e.g., Sanchiz and Barbadillo, 2007; Sanchiz and Bailon, 2013; Blain et al., 2013). Due to the problems in the paleontological literature of differentiating between *R. temporaria* and *Rana iberica* by osteological criteria (e.g., Zubeldia et al., 2007; Murelaga et al., 2011; Garcia-Ibaibarriaga et al., 2015), these two species have been grouped together as *R. temporaria-iberica* in the data matrix of the northern region. The citations of *Elaphe* sp., a snake genus that previously grouped together the current species *Zamenis scalaris* and *Zamenis longissimus*, have been assigned to *Z. scalaris* in the cases from Las Orcillas 1 and Lloma de Betxí, in accordance with the Iberian thermophilic tendencies of the herpetofaunal associations from their respective levels (Fernández et al., 2010; Tormo and De Pedro, 2013).

There are 20 levels with herpetofaunal record that have not been included in the matrix data. The chelonian citations from the paleo-archaeological sites of Gruta da Oliveira, Foz do Enxarrique, Abrigo de la Quebrada, Abric del Pastor, Cueva de San Luís, Cova Canet, Gruta do Escoural, Cova de l'Or, Ereta del Pedregal, Pic dels Corbs, Roca dels Bous, Cova del Gegant, Cova del Teixò, Can Sadurní, La Draga, Pont de Sadernes, El Pasteral, Cal Tintorer and Bòbila Madurell, as well as levels NV13, NM14 and NM4-2 of Cueva de Nerja (Jiménez Fuentes, 1986; Fernández Peris and Martínez Valle, 1989; Pérez Ripoll, 1990; Jiménez-Fuentes et al., 1998; Gómez and Jiménez Fuentes, 1998; Brugal and Raposo, 1999; Crespo, 2002; Mora et al., 2003; Budó et al., 2005; Félix et al., 2006; Morales and Sanchis, 2009; Aura et al., 2010; Jordá et al., 2011; Daura and Sanz, 2012; Sanchis et al., 2013, 2015; Pérez Ripoll, com. pers.), the citation of *Tarentola mauritanica* from level A.sup of Cova Colomera (López-García et al., 2010a), the citation of *R. iberica* from Cueva Millán (Esteban and Sanchiz, 1990) and the citation of *C. chamaeleon* from Cueva de Rincón de la Victoria (Talavera and Sanchiz, 1983) have been excluded from the northeastern and central-southern data matrices, to avoid statistical deviations owing to the large number of mono-specific citations without any other herpetofaunal taxa, although they are included in the subsequent discussion. Also, the citations of the genus *Testudo* that date from the Holocene of the northeastern area (Budó et al., 2005) have not been included because of the taxonomic revision they have undergone (Félix et al., 2006; Morales and Sanchis, 2009).

In order to compare the fossil record with the current situation, we have collected data on the present-day herpetofaunal assemblages from the same 10 × 10 km UTMs as the archaeo-paleontological sites included in the regional data matrices, through the "Especies por UTM" (species per UTM) function of the SIARE application website (Sistema de Información de Anfibios y Reptiles de España) (AHE, 2016).

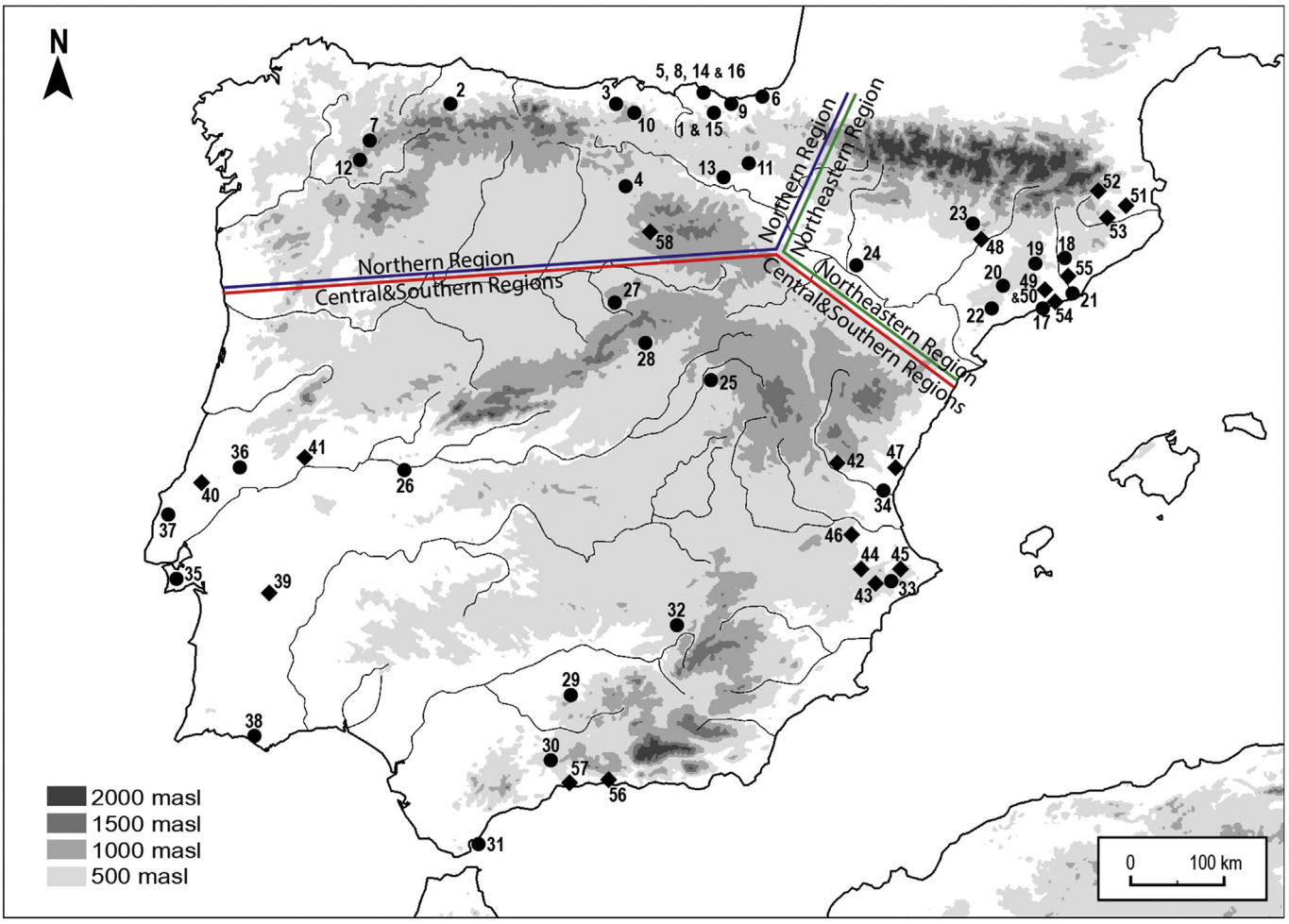

Fig. 1. Map with the latest Pleistocene-Late Holocene archaeo-paleontological sites mentioned in the text: 1) Askondo, 2) Cueva del Conde, 3) Cueva de Cobrante, 4) El Portalón, 5) Santimamiñe, 6) Erralla, 7) Valdavara-1, 8) Laminak II, 9) Aizkoltzo, 10) El Mirón, 11) Las Orcillas-1, 12) Cova Eirós, 13) Peña Larga, 14) Antoliñako Koba, 15) Dolmen of Errekatxuetako Atxa, 16) Santa Catalina, 17) Cova del Gegant, 18) Cova Teixoneres, 19) Abric Romaní, 20) Cova dels Xaragalls, 21) Riera de Canyars, 22) Cova dels Galls Carboners, 23) Cova Colomera, 24) Balsa la Tamariz, 25) Cueva de los Torrejones, 26) Sala de las Chimeneas of Maltravieso, 27) Peña de Estebanvela i, 28) Ventana, 29) Sima de Abraham, 30) Boquete de Zafarraya, 31) Gorham's Cave, 32) Castillejo del Bonete, 33) Abric del Salt, 34) Lloma de Betxí, 35) Gruta da Figueira Brava, 36) Gruta do Caldeirão, 37) Gruta Nova da Columbeira, 38) Guia of Albufeira, 39) Gruta do Escoural, 40) Gruta da Oliveira, 41) Foz do Enxarrique, 42) Abrigo de la Quebrada, 43) Abric del Pastor, 44) Cova Canet, 45) Cova de l'Or, 46) Ereta de Pedregal, 47) Pic dels Corbs, 48) Roca dels Bous, 49) Cova del Toixò, 50) Can Sadurní, 51) La Draga, 52) Pont de Sadernes, 53) El Pasteral, 54) Cal Tintorer, 55) Bòbila Madurell, 56) Cueva de Nerja, 57) Cueva de Rincón de la Victoria and 58) Cueva Millán. The sites marked with a circle are those included in the regional data matrices, while those marked with a rhombus have been excluded from them.

2.2. Classification of levels

The 118 levels have been grouped, in accordance with the geographical situation of the 38 different paleo-archaeological sites (Fig. 1; Table 1), into three data matrices (Appendix A, B & C). In each data matrix, species with a regional fossil record have been grouped into the rows, while the archaeo-paleontological levels, with their corresponding taxonomic lists, have been grouped into the columns. Therefore, in the binary data base the presence of a taxon is marked by "1" and its absence by "0". The three resultant data matrices are:

Northern Region: this includes 16 sites located between Galicia and Navarra, covering the entire Cantabrian fringe and inner area as far as Portalón de Atapuerca at its southern boundary. This region is currently characterized by a humid climate due to the Atlantic influence, with rather cold winters and temperate summers. Overall, there is a good distribution of levels throughout the studied period and all the archaeological cultures known for this region are represented: the Mousterian associated with *Homo neanderthalensis* and the Aurignacian, Gravettian, Solutrean, Magdalenian, Azilian, Microlaminar Epipaleolithic, Mesolithic, Neolithic, Chalcolithic and Bronze Age that are linked to Anatomically Modern Man. A total of 75 archaeo-paleontological levels (Table 1) and 24 different taxa have been included in the data matrix for the northern region (Appendix A).

Northeastern Region: this includes 8 sites located in present-day Catalonia and Aragon, from the Mediterranean to the Pyrenees and the Middle Ebro River Valley, in the northern area of the Mediterranean side of Iberia. Most of these sites are dated to MIS 3 while most of the MIS 1 records are mono-specific chelonian citations, which have not been included in the data matrix. At present, there are no sites in this area with published herpetofauna dated to MIS 2. The human cultures represented in the total of 23 archaeological levels (Table 1) are Mousterian, Neolithic and Bronze Age and 17 different herpetofaunal taxa have been included in the data matrix for the northeastern zone (Appendix B).

Central and Southern Regions: this group includes 14 sites in the Mediterranean area, mainly distributed in Castilian and Extremaduran areas, Andalusia, central and southern Portugal, and the center of the Valencia Country. The human cultures represented in

Table 1
- List of the latest Pleistocene-Late Holocene archae-paleontological sites and levels included in the regional data matrices. Regions: *N*, Northern region; *NE*, Northeastern region; *C&S*, Central and Southern regions.

Sites	Levels	Region	References
1. Askondo	13, 9, 8, 7, 6, 5, 3, 2 & 1	N	Garete and Rios-Garaizar, 2011; Garcia-Ibaibarriaga et al., 2015
2. Cueva del Conde	N104, N103, N10b, N20a, N2a1 & N2a2	N	Arbizu et al., 2005; López-García et al., 2011c
3. Cobrante	N7 to N1	N	Rasines, 2009; Martín et al., 2009
4. Portalón de Atapuerca	P16 to P1	N	Carretero et al., 2008; Ruíz-Zapata et al., 2008; López-García et al., 2010b
5. Cova Eirós	3 & 2	N	Rey-Rodríguez et al., 2016
6. Antoliñako Koba	D, C, B & A	N	Zubeldia et al., 2007
7. Santimamiñe	Arg-o, Camr, Csn, Balm, Almp, Slnc, Arcp, Slm & Lsm	N	Murelaga et al., 2011; Rofes et al., 2014
8. Erralla	VI, V, IV, III & II	N	Esteban and Sanchiz 1985; Peman 1985; Altuna 1985
9. Valdavara-1	Lower & Upper Units	N	Vaquero et al., 2009; Blain et al., 2009b; López-García et al., 2011b
10. Santa Catalina	III, II & I	N	Arribas and Berganza, 2010; Bailon and García-Ibaibarriaga, 2014
11. Laminak II	II-I	N	Arribas and Berganza, 1989; Sanchiz and Esteban 1994; Peman, 1994; Berganza and Arribas, 1994
12. Aizkoltzo	L.15-12	N	Murelaga et al., 2008
13. El Mirón	10 to 3	N	Straus et al., 2001; Sanchiz et al., 2012
14. Las Orcillas-1	C.II-I	N	Fernández et al., 2010
15. Peña Larga	IV-I	N	Castaños 1997; Murelaga et al., 2009; Rofes et al., 2013
16. Errekatxuetako Atxa's Dolmen	Bell Beaker level	N	Murelaga et al., 2007
17. Teixoneres	IIb & II	NE	Tissoux et al., 2006; Rosell et al., 2010, 2014; López-García et al., 2012b, 2014a
18. Cova del Gegant	V, IV & III	NE	Daura et al., 2005, 2010; Daura and Sanz, 2012; López-García et al., 2007, 2008, 2012a, 2014a
19. Abric Romaní	O, K, J, E & D	NE	Burjachs and Julià, 1994; Burjachs et al., 2012; López-García et al., 2014a
20. Xaragalls	C8 to C3	NE	López-García et al., 2012c
21. Terrassa de la Riera dels Canyars	Fluvial deposit	NE	Daura et al., 2013; López-García et al., 2013, 2014a
22. Galls Carboners	L.108-105	NE	López-García et al., 2014b
23. Cova Colomera	C15, C14–15, C12 & EE1	NE	Oms et al., 2009; López-García et al., 2010a
24. Balsa la Tamariz	Burial sites and prehistoric settlement	NE	Royo and Rey, 1993; Rey and Royo, 1993; Laplana and Cuenca-Bescós, 1995
25. Cueva de los Torrejones	L.5-4	C&S	Arribas et al., 1995, 1997
26. Sala de las Chimeneas, Maltravieso	A	C&S	Rodríguez et al., 2009; Bañuls-Cardona et al., 2012
27. Peña de Estebanvela	VI, IV, III, II & I	C&S	Sanchiz and Barbadillo, 2007; Sanchiz and Bailon, 2013; Cacho et al., 2013
28. Cueva de la Ventana	Units 7-9-16-22-26, 14-18-26 & 3-4	C&S	Sánchez Marco et al., 2005
29. Sima de Abraham	Deposit 11	C&S	Martínez-Sánchez et al., 2010, 2012
30. Boquete de Zafarraya	Unit Id-Ia	C&S	Barroso and Bailon, 2003; Barroso et al., 2003; Zilhao, 2006
31. Gorham's Cave	IV, IIIb & IIIa	C&S	Gleed-Owen, 2001; Finlayson et al., 2006; Jennings et al., 2011; López-García et al., 2011a; Blain et al., 2013
32. Castillejo del Bonete	Sedimentary filling of the burial tumulus	C&S	Benítez de Lugo et al., 2016
33. Cova del Salt	XI	C&S	Pérez Luís, 2014
34. Lloma de Betxí	Bronze Age settlement	C&S	De Pedro, 2004; Tormo and De Pedro, 2013
35. Gruta da Figueira Brava	Mousterian sequence	C&S	Crespo et al., 2000; Lapparent de Broin and Antunes, 2000; Crespo, 2002
36. Gruta do Caldeirão	Mousterian sequence	C&S	Crespo, 2002
37. Gruta Nova da Columbeira	Mousterian sequence	C&S	Jiménez Fuentes et al., 1998; Crespo, 2002
38. Guia de Albufeira	Postglacial pleistocenic sequence	C&S	Crespo, 2002

the 22 archaeological levels (Table 1) are the Mousterian, Solutrean, Magdalenian, Epipaleolithic, Neolithic, the Motillas Culture and the Valencian Bronze Culture. In the data matrix for these areas 29 different taxa have been included (Appendix C).

2.3. Statistical methodology

The method of hierarchical clustering has been chosen to perform the statistical analysis, because this generates a dendrogram that reveals the relationships of similarity and difference between the species concurring in the archaeo-paleontological levels included in the data matrices. The aim is to infer whether or not the resulting herpetofaunal groups are based on chronostratigraphic criteria whose origins are related to possible biogeographic changes. In addition, the Jaccard similarity index has been applied, since this is recommended for clustering binary data, because it gives more importance to joint occurrences in the assemblages (Hammer et al., 2001). Also, the "unweighted pair-group average" has been applied to the three data matrices, resulting in the union in the dendrogram of different groups based on the average distance between their members.

Moreover, a correspondence analysis (CA) has been used to support the results of the hierarchical clustering. The CA is the recommended method for comparing associations (assigned to columns) with the total count of taxa, or identifying taxa (assigned to rows) through the associations (Greenacre, 2010). In the case of this paper its aim is to mark the relationships of proximity between taxa of different associations, grouping them closely in contrast to the more atypical taxa, which will appear in an eccentric position in relation to the rest of the set. The Paleontological Statistics program (PAST3) has been used for all statistical approaches (Hammer et al., 2001).

3. Results

A preliminary analysis of the data matrices shows clear differences in the typical composition of the three analyzed areas. For the prehistoric sequence of the northern region the most representative species are *R. temporaria* (or *R. temporaria-iberica*) (present in 69 assemblages, 90.8% of the total), *Anguis fragilis* (35 assemblages, 46.1%), *Bufo spinosus* (32 assemblages, 42.1%) and to a lesser extent *Bufo calamita* (29 assemblages, 38.1%), the genus *Alytes* (27

assemblages, 35.5%) and the genus *Vipera* (19 assemblages, 25%) (Appendix A), forming a typical association of forest environments and wet meadows. For the northeastern Iberian area the most significant taxa are *B. calamita* (13 assemblages, 56.5%), *R. temporaria* (12 assemblages, 52.2%), *Alytes obstetricans* (11 assemblages, 47.8%) and *A. fragilis* (10 assemblages, 43.5%) and to a lesser extent *B. spinosus* (9 assemblages, 39.1%), *Coronella girondica* (8 assemblages, 34.8%) and *Pelodytes punctatus* (8 assemblages, 34.78%) (Appendix B), which form a herpetofaunal association with a marked preference for humid environments and high rainfall, with the exception of *C. girondica*.

Both zones located in the northern third of the Iberian Peninsula share a herpetofauna with hygrophilous tendencies and a predilection for humid environments. However, the prevalence of *B. calamita* at the expense of *R. temporaria* in the northeastern region, coupled with the significant presence of *P. punctatus* and *C. girondica*, can be related to the greater influence of Mediterranean environments, correlated with its geographical position in the Western Mediterranean basin.

In contrast, a Mediterranean influence and thermophilic tendencies become more evident in the herpetofaunal fossil record of the remaining two thirds of the Iberian Peninsula, comprising the central, eastern and southern areas. In these regions the predominant species are *B. calamita* (15 assemblages, 68.2%), *Timon lepidus* (14 assemblages, 63.6%), *B. spinosus* (11 assemblages, 50%), *Z. scalaris* (10 assemblages, 45.4%) and in lesser measure *Pelobates cultripes* (8 assemblages, 36.4%), *Testudo hermanni* (8 assemblages, 36.4%), *Malpolon monspessulanus* (7 assemblages, 31.8%), *Pleurodeles waltl* (6 assemblages, 27.3%) and *Vipera latastei* (6 assemblages, 27.3%) (Appendix C). Together, these species are a typical association in current Mediterranean dry environments with a water regime that is markedly seasonal and the presence of open environments, scrubs and forests.

Application of the statistical analysis methods CA and hierarchical clustering to the three data matrices shows remarkable and consistent trends between the two methods. In the northern region the resulting cluster distinguishes three groups (Fig. 2A). The first group is formed by the species *B. calamita*, *B. spinosus*, *R. temporaria-iberica*, *A. fragilis* and the genera *Alytes* and *Vipera*, an association of generalist herpetofauna that is tolerant to Euro-Siberian conditions. In addition, these taxa are the only ones present in the fossil record of the Cantabrian fringe during MIS 2, the last glacial phase, and they are almost exclusive during MIS 3. The second cluster group is composed of the species *Coronella austriaca*, *Natrix maura*, *Chalcides striatus*, *I. alpestris*, *C. girondica*, *Hierophis viridiflavus*, *Lissotriton helveticus*, *Natrix natrix*, *Z. longissimus*, *Salamandra salamandra* and the genera *Hyla* and *Lacerta*. With the exception of *S. salamandra*, which has a fossil record from Cueva del Conde in MIS 3 (López-García et al., 2011c), all are hygrophilous and/or generalist taxa, tolerant to a Euro-Siberian influence, which appear in the regional fossil record during MIS 1, i.e. during the last postglacial and interglacial stages. Finally, the third group in the regional cluster is formed by *Chioglossa lusitanica*, *Discoglossus galganoi*, *T. lepidus*, *Z. scalaris* and *M. monspessulanus*. These five species also appear in the fossil record of the Iberian North during MIS 1. Except for *C. lusitanica*, which is a salamander endemic to the northwestern Iberian region (Vences, 2002), the remaining taxa are thermophilic species linked to the Mediterranean influence. This is due to the presence of the unique fossil record of *C. lusitanica* in the herpetofaunal assemblage of the Upper Unit of Valdavara-1, where also appears another thermophilic herpetofauna as *D.* cf. *galganoi*, *T. lepidus* and *M. monspessulanus* (Blain et al., 2009b; López-García et al., 2011b).

The same overview is obtained by CA, the same three groups appearing in the graphical representation of CA (Fig. 2B). The species present in the northern assemblages in MIS 3 and MIS 2 have been grouped in the right half of the graph. *S. salamandra*, absent in MIS 2 but present in MIS 3, appears in the graph in a slightly eccentric position relative to the rest of the group of hygrophilous and/or generalist species of MIS 1, but it is not grouped together with the taxa of the glacial phase, which are located in the right third of the graph.

For the northeastern Iberian region the same scenario as in the northern zone is partially repeated, although the lack of a herpetofaunal record for MIS 2 rules out any further comparison between these two Iberian regions. In the northeastern cluster the tripartite scheme is repeated (Fig. 3A). The first group is formed by *P. cultripes*, *T. lepidus*, *Z. scalaris* and *M. monspessulanus*, thermophilic species of Mediterranean influence that appear in the regional record in MIS 1, even though *P. cultripes* has a previous record in MIS 3 (López-García et al., 2012a). The second group is formed by the species that occur in the fossil record of this region for MIS 3: *S. salamandra*, *A. obstetricans*, *P. punctatus*, *B. calamita*, *B. spinosus*, *R. temporaria*, *A. fragilis*, *C. austriaca*, *C. girondica*, *Vipera aspis* and *V. latastei*. The third group is composed of *N. maura* and *C. asper*, which appear in the regional record in MIS 1. *N. maura* is a water snake with generalist trends, while *C. asper* is a newt endemic to the Pyrenees Mountains. Applying CA to the same data matrix shows a clear separation of thermophilic Mediterranean species with respect to the other taxa. It also shows a position near the binomial *C. asper* and *N. maura* for the conjunction of species from MIS 3, though separated from them, in correlation with the hygrophilous, tolerant tendencies of both groups (Fig. 3B).

Finally, for the central-southern quadrants of the Iberian Peninsula, the dendrogram is much less clear compared to the previous two. In this case the different groups do not correspond to chronological criteria, suggesting possible stability in the composition of the herpetofaunal fossil record of this region, which is entirely composed of typical Iberian Mediterranean species (Fig. 4.A). However, the existence of potential biases in the fossil record and/or data matrix cannot be ruled out. These could be indicated in the cluster by the position of the three chelonian species, which are only represented in the data matrix by citations in assemblages in archaeo-paleontological levels, although the quantity of mono-specific citations is higher in the literature. Nonetheless, if these three taxa are excluded, the scenario expounded by the CA allows the existence of a single large group of taxa to be distinguished. The exceptions are the species *S. salamandra* and *Psammodromus algirus* and the genus *Alytes* because of their eccentric positions relative to the other taxa, though they orbit around the main group (Fig. 4.B). In the case of *P. algirus*, which is an abundant species in the Mediterranean bioregion, this is possibly due to the difficulty of documenting its presence in the fossil record because of the problems in identifying the diagnostic osteological characters, resulting in a small number of citations in the assemblages. In the cases of *S. salamandra* and *Alytes* this may be due to their more hygrophilous tendencies in contrast to the rest of the taxa in the region, which provides a dry and thermophilic context that is in principle less suitable for these amphibians.

Comparing the data with the current situation, in the total of 14 10×10 km UTMs where the archaeo-paleontological sites included in the data matrix of the northern region are located, the following species are present: *B. spinosus* (14 assemblages, 100% of the total); *A. fragilis* and *A. obstetricans* (13 assemblages, 92.8%); *L. helveticus* and *N. maura* (12 assemblages, 85.7%); *Pelophylax perezi*, *Podarcis liolepis* and *S. salamandra* (11 assemblages, 78.6%); *Lacerta bilineata*, *N. astreptophora*, *Podarcis muralis*, *R. temporaria* and *Vipera seoanei* (10 assemblages, 71.4%); *Triturus marmoratus* (9 assemblages, 64.3%); *C. striatus*, *Lacerta schreiberi* and *Z. vivipara* (8 assemblages,

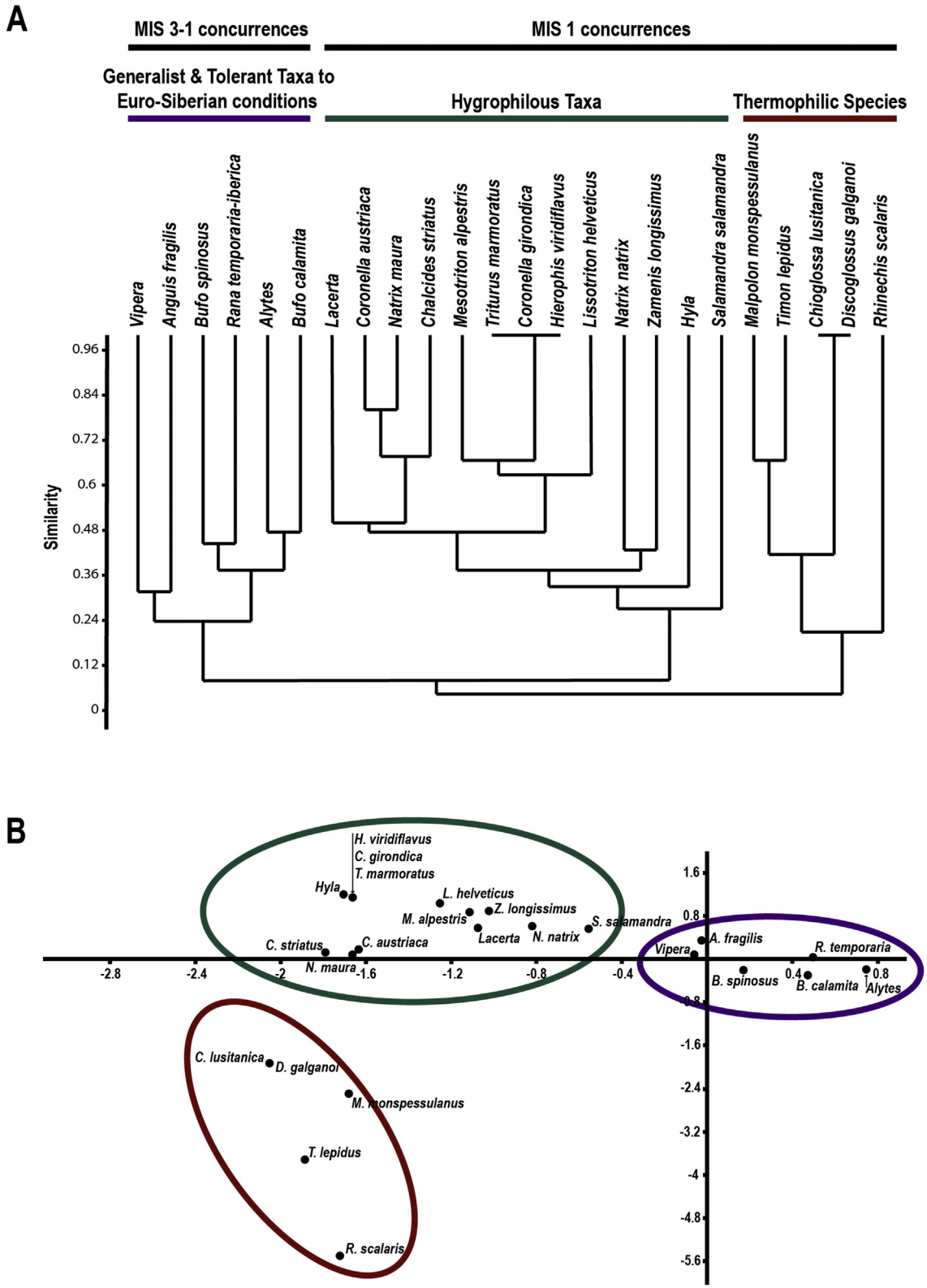

Fig. 2. - Northern Iberian herpetofaunal record: A) dendrogram of the cluster analysis with the Jaccard similarity index, and B) graphical representation of the correspondence analysis of latest Pleistocene-Late Holocene assemblages.

57.1%); *C. austriaca* (7 assemblages, 50%); *C. girondica* and *R. iberica* (6 assemblages, 42.8%); *Z. longissimus* and *T. lepidus* (5 assemblages, 35.7%); *B. calamita*, *D. galganoi*, *Hyla molleri* and *I. alpestris* (4 assemblages, 28.6%); *Mauremys leprosa* and *Z. scalaris* (3 assemblages, 21.4%); *Iberolacerta monticola*, *Lissotriton boscai*, *M. monspessulanus*, *P. punctatus*, *Podarcis bocagei*, *P. algirus* and

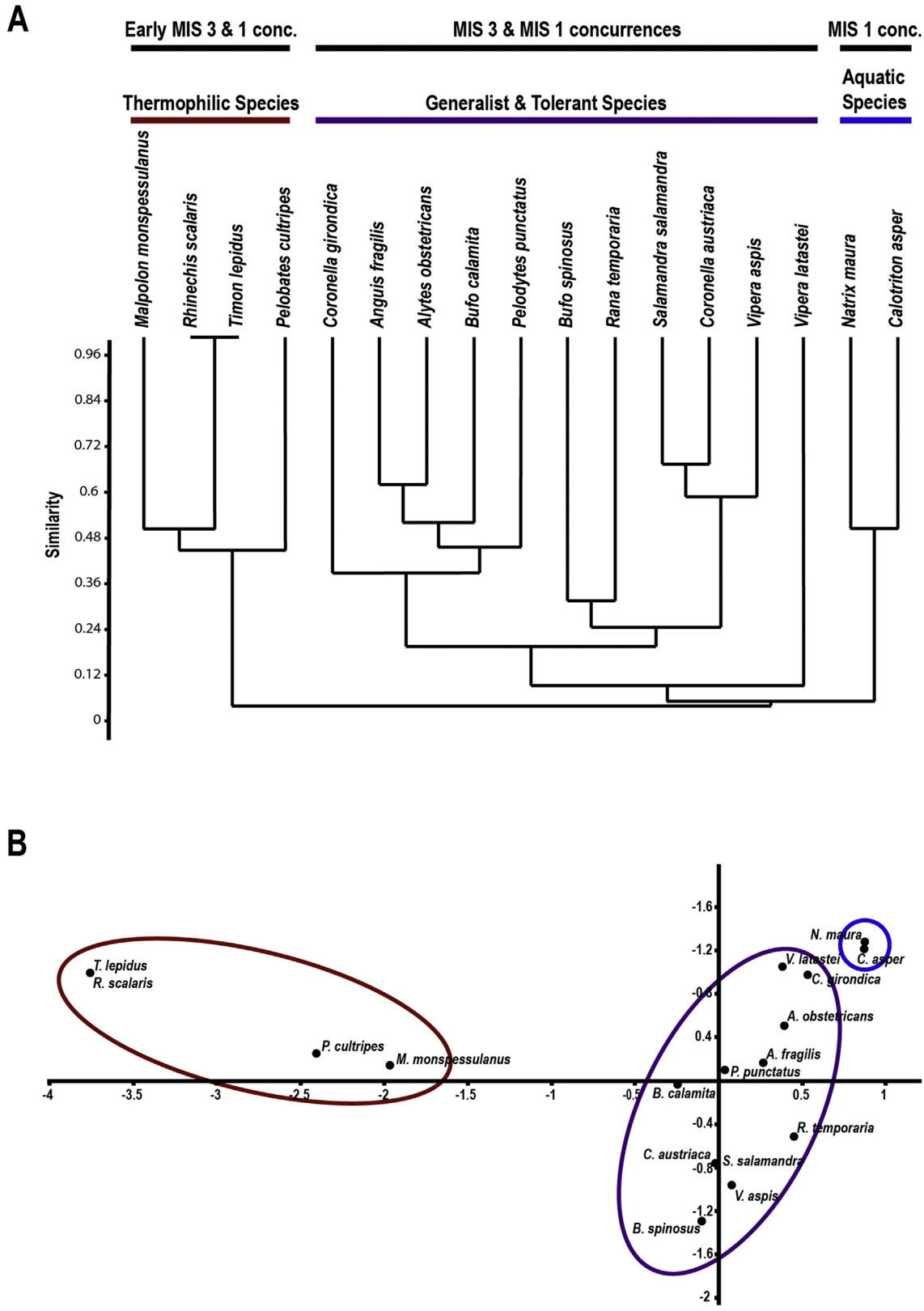

Fig. 3. - Northeastern Iberian herpetofaunal record: A) dendrogram of the cluster analysis with the Jaccard similarity index, and B) graphical representation of the correspondence analysis (C) of latest Pleistocene-Late Holocene assemblages.

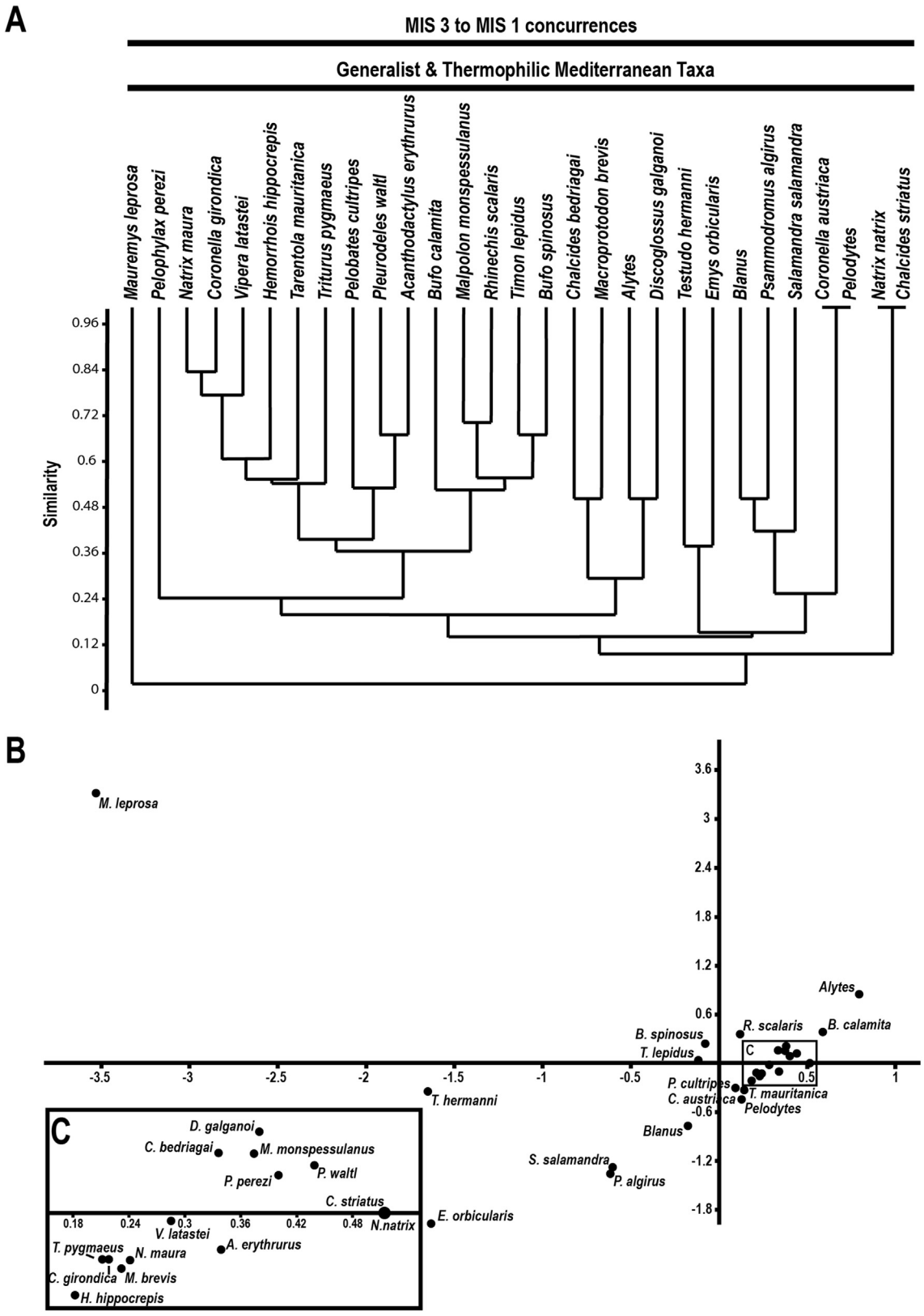

Fig. 4. - Central and southern Iberian fossil records: A) dendrogram of the cluster analysis with the Jaccard similarity index, and B) graphical representation of the correspondence analysis, with enlarged detail (C), of the latest Pleistocene-Late Holocene assemblages.

V. aspis (2 assemblages, 14.3%); *B. cinereus*, *C. lusitanica*, *Emys orbicularis*, *Rana dalmatina* and *V. latastei* (1 assemblage, 7.1%) (Table 2) (based on AHE, 2016).

At present, at a specific level, *Z. vivipara*, the different species of the genus *Podarcis*, *P. algirus*, *H. molleri*, *E. orbicularis*, *M. leprosa*, *B. cinereus*, *V. aspis*, *V. latastei*, *L. boscai*, *P. punctatus*, *P. perezi*, *L. bilineata*, *L. schreiberi* and *I. monticola* have no fossil record in the latest Quaternary in the Cantabrian region. By contrast with its absence in the fossil record, *P. perezi* is notable for its high presence in the current assemblages, although the available genetic studies have not suggested applicable paleobiogeographical scenarios for the region studied here (Hotz et al., 1994; Arano et al., 1995; Montori, 2014).

In the northeastern region the current situation is very different from the latest Quaternary herpetofauna as known until now, especially for MIS 3. Thus, in the 8 current assemblages located in the same 10 × 10 km UTMs as the sites included in the northeastern area of the Iberian Peninsula, the following species are present: *B. calamita*, *B. spinosus*, *M. monspessulanus*, *P. perezi*, *P. liolepis*, *P. algirus* and *T. lepidus* (8 assemblages, 100%); *A. obstetricans*, *N. maura*, *Z. scalaris*, *S. salamandra* and *T. mauritanica* (7 assemblages, 87.5%); *C. girondica*, *N. astreptophora* and *P. punctatus* (6 assemblages, 75%); *A. fragilis* and *V. latastei* (5 assemblages, 62.5%); *Hyla meridionalis*, *M. leprosa*, *P. cultripes* and *Psammodromus*

Table 2
Comparison between latest Pleistocene-Late Holocene (MIS3-MIS1) and present-day herpetofaunal assemblages from the same 10 × 10 km UTMs as the archaeo-paleontological sites included in the regional data matrices.

	Northern region		Northeastern region		Central & Southern regions	
	MIS 3 – MIS 1	Today	MIS 3 – MIS 1	Today	MIS 3 – MIS 1	Today
≥ 75% to 100%	*R. temporaria-iberica*	*A. obstetricans* *A. fragilis* *B. spinosus* *L. helveticus* *N. maura* *P. perezi* *P. liolepis* *S. salamandra*		*A. obstetricans* *B. calamita* *B. spinosus* *C. girondica* *M. monspessulanus* *N. maura* *P. perezi* *P. waltl* *P. algirus* *Z. scalaris* *T. mauritanica* *T. lepidus*		*B. calamita* *B. spinosus* *M. monspessulanus* *N. maura* *N. astreptophora* *P. punctatus* *P. perezi* *P. liolepis* *P. algirus* *Z. scalaris* *S. salamandra* *T. mauritanica* *T. lepidus* *V. latastei*
≥ 50% to < 75%		*C. striatus* *C. austriaca* *L. bilineata* *L. schreiberi* *N. astreptophora* *P. muralis* *R. temporaria* *T. marmoratus* *V. seoanei* *Z. vivipara*	*B. calamita* *R. temporaria*	*A. fragilis* *H. meridionalis* *M. leprosa* *P. cultripes* *P. edwardsianus* *V. latastei*	*B. calamita* *B. spinosus* *T. lepidus*	*C. girondica* *H. hippocrepis* *M. leprosa* *N. astreptophora* *P. cultripes* P. *hispanicus*
≥ 25% to < 50%	*Alytes* *A. fragilis* *B. spinosus* *B. calamita* *Vipera*	*B. calamita* *C. girondica* *D. galganoi* *H. molleri* *I. alpestris* *R. iberica* *T. lepidus* *Z. longissimus*	*A. obstetricans* *A. fragilis* *B. spinosus* *C. girondica* *P. punctatus*	*C. striatus* *H. turcicus* *H. hippocrepis* *P. muralis*	*M. monspessulanus* *P. cultripes* *P. waltl* *Z. scalaris* *T. hermanni* *V. latastei*	*A. obstetricans* *B. cinereus* *C. bedriagai* *C. striatus* *D. galganoi* *H. turcicus* *H. meridionali* *H. molleri* *P. guadarramae* *T. pygmaeus*
< 25%	*C. striatus* *C. lusitanica* *C. austriaca* *C. girondica* *D. galganoi* *H. viridiflavus* *Hyla* *Lacerta* *L. helveticus* *M. monspessulanus* *I. alpestris* *N. maura* *N. natrix* s.l. *Z. scalaris* *S. salamandra* *T. lepidus* *T. marmoratus* *Z. longissimus*	*B. cinereus* *C. lusitanica* *E. orbicularis* *I. montícola* *L. boscai* *M. monspessulanus* *M. leprosa* *P. punctatus* *P. bocagei* *P. algirus* *R. dalmatina* *Z. scalaris* *V. aspis* *V. latastei*	*C. asper* *C. austriaca* *M. monspessulanus* *N. maura* *P. cultripes* *Z. scalaris* *S. salamandra* *T. lepidus* *V. aspis* *V. latastei*	*D. pictus* *L. helveticus* *T. marmoratus* *V. aspis* *Z. longissimus*	*A. erythrurus* *Alytes* *Blanus* *C. bedriagai* *C. striatus* *C. austriaca* *C. girondica* *D. galganoi* *E. orbicularis* *H. hippocrepis* *M. brevis* *M. leprosa* *Natrix maura* *N. natrix* s.l. *Pelodytes* *P. perezi* *P. algirus* *S. salamandra* *T. mauritanica* *T. pygmaeus*	*A. erythrurus,* *A. cisternasii* *A. dickhilleni* *C. chamaeleon* *E. orbicularis* *L. schreiberi* *L. boscai* *M. brevis* *P. ibericus* *P. punctatus* *P. hispanica* *P. vaucheri* *P. virescens* *P. edwardsianus* *S. salamandra* *T. marmoratus*

edwardsianus (4 assemblages, 50%); *C. striatus* (3 assemblages, 37.5%); *H. turcicus*, *H. hippocrepis* and *P. muralis* (2 assemblages, 25%); *Discoglossus pictus*, *L. helveticus*, *T. marmoratus*, *V. aspis* and *Z. longissimus* (1 assemblage, 12.5%) (Table 2) (AHE, 2016). *P. perezi*, *P. liolepis*, *P. algirus*, *Z. scalaris*, *H. meridionalis*, *P. edwardsianus*, *H. turcicus*, *H. hippocrepis*, *P. muralis*, *D. pictus*, *L. helveticus*, *T. marmoratus* and *Z. longissimus* are species absent from the prehistoric record of the Late Quaternary in the northeastern Iberian area. The turtles *T. hermanni*, *M. leprosa* and *E. orbicularis* have a fossil record in northeastern Iberia during the latest Pleistocene and Holocene, although they are mono-specific citations that have been excluded from the regional data matrix (Mora et al., 2003; Budó et al., 2005; Félix et al., 2006; Morales and Sanchis, 2009; Daura and Sanz, 2012).

For the southern and central regions, the following species are present in the nine current assemblages located in the same 10 × 10 km UTMs as the sites included within the limits of the Spanish State: *B. calamita*, *B. spinosus*, *N. maura*, *P. perezi*, *P. algirus*, *Z. scalaris* and *T. lepidus* (9 assemblages, 100%); *M. monspessulanus* and *T. mauritanica* (8 assemblages, 88.89%); *P. waltl* and *V. latastei* (7 assemblages, 77.78%); *C. girondica*, *H. hippocrepis*, *M. leprosa*, *N. astreptophora* and *P. cultripes* (6 assemblages, 66.67%); *Psammodromus hispanicus* (5 assemblages, 55.55%); *B. cinereus*, *Chalcides bedriagai*, *D. galganoi*, *H. turcicus* and *H. molleri* (4 assemblages, 44.44%); *A. obstetricans*, *C. striatus*, *H. meridionalis*, *Podarcis guadarramae* and *Triturus pygmaeus* (3 assemblages, 33.33%); *A. erythrurus*, *E. orbicularis*, *L. schreiberi*, *Macroprotodon brevis*, *Pelodytes ibericus*, *P. punctatus*, *Podarcis hispanica*, *Podarcis vaucheri*, *Podarcis virescens*, *P. edwardsianus*, *S. salamandra* and *T. marmoratus* (2 assemblages, 22.22%); *Alytes cisternasii*, *Alytes dickhilleni*, *C. chamaeleon* and *L. boscai* (1 assemblage, 11.11%) (Table 2) (AHE, 2016).

The different species of the genera *Podarcis* and *Hyla*, as well as the species *A. dickhilleni*, *A. obstetricans*, *H. turcicus*, *L. schreiberi*, *L. boscai*, *P. ibericus*, *P. edwardsianus*, *P. hispanicus* and *T. marmoratus*, are without citations at a specific level in the central-southern fossil record for the period between MIS 3 and MIS 1.

4. Discussion

4.1. Cantabrian northern region

The most representative taxa for the prehistoric sequence of the end of the Upper Pleistocene and Holocene in the northern Iberian area, which ranges from Navarre to Galicia, are *B. spinosus*, *B. calamita*, *R. temporaria* (or *R. temporaria-iberica*), *A. fragilis* and the genera *Alytes* and *Vipera*, which are a typical assemblage in forest environments and wet meadows with abundant water points.

A. fragilis is a legless lizard widely distributed across Euro-Siberian Europe, which extends significantly into the northern portion of the Iberian Peninsula. It is a hygrophilous species that occupies a wide range of habitats typical of the Euro-Siberian region, especially those with a dense herbaceous stratum, although it may occasionally appear in the supra-Mediterranean and oro-Mediterranean bioclimatic levels of the Iberian Mediterranean area (Galán and Salvador, 2009), provided that the average annual rainfall exceeds 600 mm (Llorente et al., 1995). Also, its presence is negatively correlated with the number of annual hours of sunshine and with the average temperature of the warmest month, for it prefers cooler and wetter areas with the rainfall distributed throughout the year (Smith, 1998). *B. spinosus* currently prefers the forested areas of the northern Iberian area, deciduous forests with the presence of water courses and, to a lesser extent, wet meadows (Ortiz-Santaliestra, 2014). *R. temporaria* limits its distribution range to areas with temporary or permanent water points (Álvarez, 2014) and it depends on an average annual rainfall that exceeds 1100 mm in the eastern Cantabrian area (Gosá and Bergerandi, 1994).

The documented assemblages dating from MIS 3 and MIS 2 in northern Iberia stand out for the low variety of identified taxa: *S. salamandra*, *A. obstetricans*, *B. calamita*, *B. spinosus*, *R. temporaria-iberica*, *A. fragilis* and *Vipera* sp. (Zubeldia et al., 2007; Martín et al., 2009; López-García et al., 2010b, 2011c; Garcia-Ibaibarriaga et al., 2015), in addition to the citations of Ophidia indet. (López-García et al., 2010b), Colubrinae indet. (Martín et al., 2009) and Salamandridae indet. (Zubeldia et al., 2007). Compared to MIS 3, the fossil record of MIS 2 is thus notable for the absence of fossil remains from Salamandridae and Colubridae, as well as the presence of a single record of the genus *Vipera* in the fossil record for the northern area (López-García et al., 2010b). *A. fragilis*, which is widely represented in the sequences of MIS 3 and MIS 1, is only found in level Arg-o of Santimamiñe (Murelaga et al., 2011) and level C of Antoliñako Koba (Zubeldia et al., 2007). The typical association is reduced to *A. obstetricans*, *B. calamita*, *B. spinosus* and *R. temporaria-iberica* (Esteban and Sanchiz, 1985; Zubeldia et al., 2007; Martín et al., 2009; López-García et al., 2010b; Murelaga et al., 2011), with sporadic records of *A. fragilis* (Zubeldia et al., 2007; Murelaga et al., 2011), *Vipera* sp. (López-García et al., 2010b), Lacertidae indet. (cf. *Podarcis*) (Zubeldia et al., 2007; López-García et al., 2010b) and the probable *R. dalmatina* from Erralla VI (Esteban and Sanchiz, 1985).

The species present before and during the Last Glacial Maximum are mostly generalist species that can tolerate a wide climatic and environmental spectrum (*B. spinosus*, *B. calamita*, *A. fragilis* and the genera *Rana* and *Vipera*). Significantly, the northern sequence is monopolized by *R. temporaria*, a species that has a pronounced preference for humid environments and Euro-Siberian climatic conditions, and this frog species appears in all of the documented assemblages in the sequences of MIS 3 and MIS 2.

In the fossil record, significant changes are detected in the composition of herpetofaunal associations from the beginning of MIS 1. In some assemblages the number of hygrophilous and generalist species increases, while species linked to a Mediterranean influence appear in this area for the first time. The first citation of a thermophilic species in the fossil record of northern Iberia during the postglacial period is the snake *M. monspessulanus* in the Lower Unit of Valdavara-1 (15,120 ± 70 B.P.-13,770 ± 70 B.P, Vaquero et al., 2009; López-García et al., 2011b). These absolute datings situate the Lower Unit of Valdavara-1 in the warm climate phase of the Bölling-Allerød interstadial (Naughton et al., 2015) and are consistent with the presence of *M. monspessulanus*. This is a fully thermophilic snake with high thermal requirements (Cheylan et al., 1981; Blázquez and Pleguezuelos, 2002), whose appearance in the Galician area can be related to a process of colonization of the northern region from a southern Iberian *refugium* due to the rising temperatures after the end of MIS 2.

The latest Pleistocene sequence in the Lower Unit of Valdavara-1 also features the first appearance of the snakes *N. maura*, *N. natrix* (sensu lato) and *C.* cf. *austriaca* and the reappearance of *S. salamandra*, which is absent in MIS 2. Further, in this same unit the genus *Lacerta* (sensu lato) is cited for the first time in the regional record of the Late Pleistocene (López-García et al., 2011b). This is an interesting citation given that Lacerta sensu lato in the northern area includes three diferent species (*T. lepidus*, *L. schreiberi* and *L. bilineata*), which underwent three different processes of postglacial colonization according to molecular data from the Cantabrian fringe (Paulo et al., 2001, 2002a; Guedes, 2015). Therefore, greater efforts or news sub-fossil discoveries are required for their species-level assignment.

In the eastern part of the Cantabrian fringe, in the Basque

Country, the three levels with herpetofaunal assemblages from Cueva de Santa Catalina, and especially levels N.II and N.I, stand out for the high diversity of their assemblages in the early Pre-Boreal stage of the Holocene (Bailon and García-Ibaibarriaga, 2014). The newt cf. *I. alpestris* has its first record in level N.III in the final phase of the latest Pleistocene (between 12,425 ± 90 B.P. and 12,345 ± 85 B.P.), while in the Holocene level N.II (11,155 ± 80 B.P.) and level N.I (between 10,530 ± 110 B.P. and 9180 ± 110 B.P.) (Arribas and Berganza, 2010) some species previously absent from the prehistoric sequence of the Late Pleistocene appear in concurrence: cf. *L. helveticus*, *Triturus* cf. *marmoratus*, *C. striatus*, *C.* cf. *girondica*, cf. *Z. longissimus* and cf. *H. viridiflavus*. *Lacerta* sp. (= *Lacerta* sensu lato) also appears in both Holocene levels from Santa Catalina, with the same taxonomic problems as in the aforementioned case of the Lower Unit of Valdavara-1. The frog *Hyla* sp., an unprecedented genus in the regional record, appears in level N.II of Santa Catalina (Bailon and García-Ibaibarriaga, 2014).

Levels N.II and N.I of Santa Catalina provide two rich assemblages of species that currently have diverse biogeographical dynamics, which might suggest multiple colonizations in the Cantabrian area from distant and different *refugia*. However, the case of *L. helveticus* invokes caution with respect to these hypotheses. This newt is distributed from the northern third of the Iberian Peninsula to the northern tip of Great Britain and the extreme west of the Czech Republic (Schlüpmann and van Gelder, 2004). Molecular analyses have identified great genetic diversity among its Iberian populations, which are grouped into four different clades. It was exclusively the eastern clade of *L. helveticus* that carried out the postglacial colonization of Western and Central Europe, the Iberian Peninsula thus serving as its glacial refuge (Recuero and García-París, 2011). These data contrast with the apparent absence of *L. helveticus* in the northern fossil record of the Late Pleistocene, indicating that its glacial refugia were possibly located in the south.

The herpetofaunal assemblage of the archaeological site of Las Orcillas-1 in Navarre is of a later date. Concretely, the archaeological remains of levels C.II-I from Las Orcillas, which are assigned to the Microlaminar Epipaleolithic and dated to 8610 ± 50 B.P., locate the herpetofaunal assemblage in the late Pre-Boreal stage (Fernández et al., 2010). The association is formed by *B. spinosus*, *B. calamita*, *T. lepidus*, *M. monspessulanus*, *Natrix* sp. and *Zamenis-Rhinechis* (= *Elaphe* sp. sensu lato) (Fernández et al., 2010). This assemblage includes two thermophilic Mediterranean species, the lizard *T. lepidus* and the snake *M. monspessulanus*, this being the oldest Holocene record for *T. lepidus* in the northern Iberian Peninsula. It also includes the possible presence of other species typical of warm environments, such as *Z. scalaris*.

At the western end of the northern Iberian region, in Galicia, the Upper Unit of Valdavara-1 also presents a more recent assemblage with the presence of thermophilic Mediterranean species. The Upper Unit is ascribed to the Chalcolithic and is dated to 4490 ± 40 B.P. (Vaquero et al., 2009). The assemblage from this level is formed by *C. lusitanica*, *Discoglossus* cf. *galganoi*, *B. spinosus*, *R. iberica*, *C. striatus*, *A. fragilis*, *T. lepidus*, *N. maura*, *Coronella* cf. *austriaca*, *M. monspessulanus* and *Vipera* sp. (Blain et al., 2009b; López-García et al., 2011b). The frog *R. iberica*, an Iberian endemism that is ecologically very similar to *R. temporaria*, has its oldest record in level 1 of Cueva Millán, dated to MIS 3 (Esteban and Sanchiz, 1990; Díez et al., 2008), and reappears during MIS 1 in the Upper Unit of Valdavara-1. *M. monspessulanus* and *T. lepidus* appear again in association in the Upper Unit of Valdavara-1, also accompanied by another thermophilic species that makes its first postglacial appearance in the northern region, the frog *D. galganoi* (López-García et al., 2011b). *C. lusitanica* also appears for the first time in this region; this is a salamander whose distribution is currently limited to northwestern Iberia (Blain et al., 2009b). Another species typical of this region has been identified in the Upper Unit of Valdavara-1, the skink *C. striatus* (López-García et al., 2011b), which is also present in levels N.II and N.I of Santa Catalina (Bailon and García-Ibaibarriaga, 2014). The genus *Lacerta*, which has no fossil record with specific-level ascription in the Atlantic-Cantabrian region, includes another reptile typical of northwestern Iberia, *L. schreiberi*, as well as *L. bilineata* for the northern area. Large-sized lizards assigned to *Lacerta* sp. have been identified in the Lower Unit of Valdavara-1 (López-García et al., 2011b) and level 1 of Cobrante (Martín et al., 2009).

The prehistoric assemblages from Orcillas-1 and Valdavara-1 possibly indicate the existence of two colonization routes towards the north of the Iberian Peninsula for species of Mediterranean influence and for hygrophilous species less tolerant to cold climates and glacial conditions. The eastern route, represented by Orcillas-1, would consist of the Ebro Valley and, according to the fossil record, would have been used by a Mediterranean herpetofauna (e.g., *T. lepidus*, *M. monspessulanus* and possibly *Z. scalaris*). The western route, marked by Valdavara-1, would be located on the Atlantic coastline running towards the Galician coasts and would have been used by species of Mediterranean origin (e.g., *D. galganoi*, *T. lepidus* and *M. monspessulanus*) as well as typically western species (e.g., *C. lusitanica* and *L. schreiberi*), and generalist species and/or species tolerant to Euro-Siberian conditions (e.g., *N. maura* and *C. striatus*), to colonize northwestern Iberia and the Cantabrian fringe.

Given our imperfect knowledge of the fossil record, molecular genetics is a discipline that can clarify expansive movements during postglacial colonization. Molecular studies of current populations of *C. lusitanica* are consistent with the proposed scenario, with two clades separated by the River Mondego, it being the northern population that underwent a postglacial expansion towards Galicia and Asturias (Alexandrino et al., 2000, 2002, 2005, 2007). The data provided by mitochondrial DNA show the existence of four clades of *L. schreiberi*. The northwestern clade has less genetic diversity and a greater geographical distribution, related to a very rapid recent expansion (Paulo et al., 2001), an expansive colonization process also documented in its nuclear DNA (Godinho et al., 2008). In the northwestern region, a chronologically recent expansive pattern has also been documented in *P. bocagei* (Pinho et al., 2007a). By contrast, *C. striatus* shows two distinct clades, the first distributed in the south of the Iberian Peninsula and the second spanning northern Iberia, the south of France and northwestern Italy. This second clade has a uniform genetic composition with a low level of diversification, which corresponds to a rapid and recent expansion, possibly postglacial (Carranza et al., 2008). *C. girondica* also shows a similar phylogeographic pattern, with three clades in European territory: two clades are limited to the Baetic region and southwestern Iberia, in contrast to the third clade, characterized by low genetic diversity, which covers the rest of the Iberian Peninsula, southern France, and northern and central Italy, and is the result of a recent expansion (Santos et al., 2012). *N. maura* has two well-differentiated clades in the Iberian Peninsula, a southern one based in the extreme south of Andalusia and another clade found in the rest of the Iberian Peninsula, which would have also colonized central and southern France, western Switzerland and northwestern Italy in the course of the Holocene (Joger et al., 2006).

Z. longissimus is another snake that makes its first appearance in the northern area during the Holocene. This also represents its first appearance in the Iberian prehistoric record. Accordingly, its first record corresponds to levels N.II and N.I of Santa Catalina (Bailon and García-Ibaibarriaga, 2014), followed by the Aizkoltzo sequence (Murelaga et al., 2008) and the Chalcolithic level of El Mirón (Sanchiz et al., 2012). Phylogenetic analyses have suggested the expansion northwards of *Z. longissimus* during the Holocene

Climate Optimum (*ca*. 8000-5000 B.P.) from two glacial *refugia* separated by the Alps, reaching its maximum latitudinal range in the Danish Peninsula. After this warm climate phase its distribution recoiled southwards, leaving isolated present-day populations in Germany and the Czech Republic (Musilová et al., 2010). In the Iberian Peninsula it has colonized regions of the Pyrenees, in addition to which it has two separate populations, one in the Picos de Europa (Cantabria) and another in the Galician Massif which would be the result of a postglacial colonization and the subsequent retraction of its Iberian distribution (Ayllón et al., 2010; Cabana et al., 2014). The chronology of the Iberian sites with a record of *Z. longissimus*, coupled with the existence of these isolated populations, is consistent with the pattern proposed on the basis of phylogenetic studies (Musilová et al., 2010), although one might advance to the early Holocene the southern expansion of this snake. *H. viridiflavus*, another snake originating from the Italian Peninsula, which appears in levels N.II and N.I of Santa Catalina (Bailon and García-Ibaibarriaga, 2014), presents a similar phylogeography, although there are no molecular data for the Iberian populations. The closest studied populations are from France; these are the result of a recent colonization from the western Italian clade of *H. viridiflavus* (Nagy et al., 2002).

In contrast, data provided by the genetic studies of other Iberian species make caution essential when drawing conclusions based only on the fossil record as currently known. *Z. vivipara* is a Euro-Siberian lizard with a wide Palearctic distribution (Dely and Böhme, 1984), although in Iberia it is currently restricted to the Cantabrian fringe and the Pyrenees (Braña and Bea, 2002). This distribution pattern, along with its apparent absence from the Iberian fossil record, may suggest a postglacial colonization from Central Europe, where it has a fossil record during the Pleistocene (Holman, 1998). Nevertheless, phylogeographic genetic studies present a diversified situation, with five clades present in its Iberian distribution area, which were generated by vicariant processes throughout the Pleistocene (Milá et al., 2013). Similar phylogeographies are repeated in the case of two lizard taxa with an Iberian distribution, *P. muralis* (Salvi et al., 2013) and the genus *Iberolacerta* (Crochet et al., 2004). This leads us to propose a long evolutionary history within their own territory; apparent absences in the known fossil record are explained by the difficulty of their taxonomic identification from osteological characters (Barahona, 1996; Barahona and Barbadillo, 1997), making greater efforts necessary in this field. These taxa may be behind the indeterminate lizards of levels 9–7, 5 and 2 of Askondo (Garcia-Ibaibarriaga et al., 2015), levels P11-3 and P1 of El Portalón (López-García et al., 2010b), and cf. *Podarcis* of levels D, C and B of Antoliñako Koba (Zubeldia et al., 2007).

During MIS 1 significant changes are detected in the composition of the assemblages of reptiles and amphibians, though most of them are still dominated by the same species present in the sequences of MIS 3 and MIS 2: *A. obstetricans*, *A. fragilis*, *B. calamita*, *B. spinosus*, *R. temporaria* (or *R. temporaria-iberica*) and the genus *Vipera*. For example, the assemblages of levels IV, III and II of Erralla (Esteban and Sanchiz, 1985), levels *Balm*, *Almp*, *Slnc*, *Arcp*, *Slm* and *Lsm* of Santimamiñe (Murelaga et al., 2011), level 2 of Cobrante (Martín et al., 2009), levels 3 and 2 of Askondo (Garcia-Ibaibarriaga et al., 2015), level A of Antoliñako Koba (Garcia-Ibaibarriaga et al., 2015) and the Bell Beaker level of the dolmen of Errekatxuetako Atxa (Murelaga et al., 2007) are exclusively composed of taxa from the previously mentioned herpetofaunal association.

The midwife toad *A. obstetricans*, with representation through MIS 2 in the sequences from Portalón de Atapuerca (López-García et al., 2010b) and Erralla (Esteban and Sanchiz, 1985), disappears from the fossil record of the Pleistocene part of MIS 1. It then reappears in level N.1 of Cobrante, which is ascribed to the Holocene (Martín et al., 2009). Subsequently, it also appears in the Neolithic and Bronze Age levels of El Mirón (Sanchiz et al., 2012) and in the dolmen of Errekatxuetako Atxa (Murelaga et al., 2007). On an ecological level, this absence, if it genuinely occurred and is not the product of a possible taphonomic bias, could simply be correlated with the absence of permanent water points between Heinrich Event 1 and the Pre-Boreal Holocene stage. Such points are necessary for it to complete its larval stage (Bosch, 2014).

Nonetheless, this is contradicted by the presence of species closely linked to an aquatic environment such as *S. salamandra*, cf. *I. alpestris* and cf. *L. helveticus* in the latest Pleistocene sequence from Santa Catalina and Laminak II (Sanchiz and Esteban, 1994; Bailon and García-Ibaibarriaga, 2014) and the indeterminate salamander from level B of Antoliñako Koba (Zubeldia et al., 2007). The toad *B. calamita* had a greater distribution in the paleontological record than at present. Today its distribution in the Cantabrian area is very scarce and is limited to the southernmost fringe and two coastal populations in the Basque Country (Tejedo and Reques, 1997; Reques and Tejedo, 2002; Garin-Barrio et al., 2007). In the Late Quaternary record, it appears in a total of 20 assemblages: the entire sequence from Portalón de Atapuerca and Santa Catalina (López-García et al., 2010b; Bailon and García-Ibaibarriaga, 2014), levels V and IV of Erralla (Esteban and Sanchiz, 1985), levels Camr-Csn and Lsm of Santimamiñe (Murelaga et al., 2011), level Ll.15–12 of Aizkoltzo (Murelaga et al., 2008), levels C.II-I of Las Orcillas-1 (Fernández et al., 2010) and possibly levels 4 and 3 of Cobrante (Martín et al., 2009). Today *B. calamita* is absent in the vicinity of Cobrante, Aizkoltzo, Erralla, Santimamiñe and Santa Catalina, but present in the territories of Las Orcillas-1 and Portalón de Atapuerca. It is also present in the area around Valdavara-1 and Peña Larga (AHE, 2016), although it does not appear in the archaeological record of these sites.

4.2. Northeastern region

The dominant species in the latest Quaternary in the northeastern fossil record, which basically includes Catalonia and Aragon, are *A. obstetricans*, *B. calamita*, *R. temporaria*, *A. fragilis* and to a lesser extent *B. spinosus*, *C. girondica* and *P. punctatus*. This is an assemblage with hygrophilous tendencies, although the association of *B. calamita* and *P. punctatus* indicates the existence of irregularities in the water regime that may be associated with a Mediterranean influence.

R. temporaria is a Euro-Siberian frog that in the Iberian Peninsula is restricted to the area formed by the axis of the Cantabrian Mountains and the Pyrenees and within the Mediterranean region is only present in the Montseny Massif, due to the latter's Pyrenean influences (Esteban and García-París, 2002). In these regions it lives in wetlands, from mountain meadows to deciduous forests of *Quercus* and *Fagus* (Álvarez, 2014). It does not tolerate ambient temperatures over 26 °C and needs average temperatures below 5 °C in autumn and winter to carry out its reproductive cycle (Balcells, 1975). *A. obstetricans* is another anuran especially associated with high rainfall areas. Away from these, its distribution is restricted to mountainous systems or areas that allow permanent water points, because of its particularly long larval development lasting from 91 days to three years (Bosch, 2014). *C. girondica* is a snake with an extensive western Mediterranean distribution and presents great altitudinal and environmental variation, although its main ecological requirement is the presence of small lizards (genera *Psammodromus* and *Podarcis*), its main prey (Santos and Pleguezuelos, 2009). The herpetofaunal taxa present in MIS 3 are mainly generalists and species tolerant to Mediterranean conditions as well as to Euro-Siberian climates. Noteworthy is the practical absence of thermophilic taxa by contrast with the recurrent

appearance of *R. temporaria*, despite it being an area in direct contact with the Mediterranean Sea. In fact, *R. temporaria* appears outside its current distribution in the latest Pleistocene sequences of Teixoneres, Abric Romaní and Galls Carboners; this latter site is located 120 km from the current southern boundary of the *R. temporaria* distribution on the Montseny Massif. Further, the Pleistocene citations of *V. aspis* from Teixoneres and Abric Romaní lie outside its current distribution range.

Very common species in the Mediterranean area that have significant fossil records in contemporary sites in southern Iberian areas, such as the lizard *T. lepidus* or the snake *N. maura*, only appear in the northeastern region in the Holocene levels of Balsa la Tamariz (Laplana and Cuenca-Bescós, 1995) and Cova Colomera, respectively (López-García et al., 2010a). The thermophilic Mediterranean gecko *T. mauritanica* also has its only record in this latter cave, in its most recent phase (level A.sup., 3490 ± 50 B.P.) (López-García et al., 2010a). The snake *M. monspessulanus*, closely linked to the Mediterranean bioclimate, has its only record in the latest Pleistocene in level IIb of Cova Teixoneres, assigned to MIS 3 (ca. 35,000 B.P.) (López-García et al., 2012b, 2014a; Talamo et al., 2016). This snake reappears in the northeastern record until the Bronze Age level of Balsa la Tamariz (3600–3400 B.P.), where appear in concurrence with *T. lepidus* (Laplana and Cuenca-Bescós, 1995). The thermophilic assemblage from Balsa la Tamariz (*P. cultripes*, *T. lepidus* and *M. monspessulanus*) in the Ebro Valley, combined with the presence of *T. mauritanica* in the last phase from Cova Colomera, located on one of the tributaries of the River Ebro (López-García et al., 2010a), may possibly be correlated with the existence of a natural corridor along the Ebro Valley and its tributaries, from which species native to the Mediterranean area would have colonized the Iberian inland during the Holocene climatic progression.

For the newt *T. marmoratus*, absent in the regional fossil record, different routes of colonization have been proposed for its two eastern populations: the one located in the province of Girona would be the result of a postglacial colonization from Roussillon on the other side of the Pyrenees, while the populations of southern Catalonia and central Aragon would have come from the Navarra-Rioja area; this species possibly used the River Ebro to colonize as far as its final section (Llorente et al., 1995; Montori, 2014). The River Ebro would have thus served as a route running in both directions, for Mediterranean species leading inland towards the north of the Iberian Peninsula and for hygrophilous species from the north leading to the new environments that had opened up on the eastern periphery.

The snake *C. austriaca*, with a record in MIS 3 in levels IIb and II from Cova Teixoneres (López-García et al., 2012b, 2014a) and from Canyars (Daura et al., 2013; López-García et al., 2013, 2014a), is the only species present in the northeastern prehistoric record that does not appear in the current assemblages. Another species of the genus *Coronella*, *C. girondica*, which appears on levels 8 to 5 of Cova Xaragalls (López-García et al., 2012c) and C15, C14–13 and C12 of Cova Colomera (López-García et al., 2010a), is currently distributed in a greater number of assemblages and has a greater distribution range. *C. austriaca* is much less thermophilic than *C. girondica* and the altitudinal and environmental segregation of these two species has been confirmed in the Iberian Peninsula when they are in sympatry (Galán, 1988; Lizana et al., 1988; Morales et al., 2002). The absence of *C. austriaca* in areas where it was present in the past and the currently greater distribution of *C. girondica* can be correlated with altitudinal changes in the bioclimatic levels, as proposed for the sequence from MIS 5c to MIS 4 of Cueva del Camino (semi-arid climate during warm periods to a wet mid-latitude climate during cold periods) (Blain et al., 2014b).

The absence of sites dating from MIS 2 and the poor data from MIS 1 for this area of Iberia preclude a deeper evolutionary comparison of its herpetofauna. However, the ongoing studies of the microvertebrate remains from Cova Bonica, Balma del Gai, l'Arbreda and Coves del Toll will increase what is known of the composition of the herpetofauna record and its main biogeographic changes in the Catalan area during the Late Quaternary. The current herpetofaunal composition of the northeastern region suggests a postglacial recolonization of this territory by thermophilic species along the Mediterranean coast from the Valencian Country and inland through river valleys, especially the Ebro and its tributaries. In parallel, other species would have entered from the north by the Mediterranean coast and the eastern edge of the Pyrenees, originating from the south of France and the west of Italy, as seen for the Cantabrian region with *Z. longissimus*, *H. viridiflavus* and *L. bilineata*. Finally, native Pyrenean species might have used the same river valleys to penetrate into the Pre-Pyrenean foothills and the Catalan central basins that were favorable for colonization. This would have been in addition to the existence in these mountainous areas of interglacial *refugia* for species from Euro-Siberian and/or Alpine environments, as proposed for Cova Colomera and the Serra del Montsec for species such as *R. temporaria* and *A. fragilis* (López-García et al., 2010a).

4.3. Central and southern regions

B. calamita, *T. lepidus*, *B. spinosus*, *Z. scalaris* and, to a lesser extent, *P. cultripes*, *T. hermanni*, *M. monspessulanus*, *P. waltl* and *V. latastei* are the best-represented species in the paleo-archaeological sites of the central and southern Iberian Peninsula from MIS 3 to MIS 1. Together they constitute an association of herpetofauna typical of the majority of the thermophilic environments in current Mediterranean Iberia (with the exception of *T. hermanni*, extinguished regionally). As mentioned above, they form an assemblage with a predilection for dry Mediterranean environments with a markedly seasonal water regime and the presence in the landscape of both open areas and scrubland and forests.

The large lizard *T. lepidus* is one of the most characteristic species of the Mediterranean bioclimate in southwestern Europe, to the extent that the northern boundary of its distribution coincides with the boundary between Mediterranean and Euro-Siberian bioclimates (Cheylan and Grillet, 2005). *B. spinosus* is a very generalist toad that occupies practically all habitats characteristic of the Iberian Peninsula, from the thermo-Mediterranean pre-montane areas to the Euro-Siberian mountains (Ortiz-Santaliestra, 2014), while *B. calamita*, also generalist and fairly widespread, prefers open areas with sparse vegetation or low cover and high insolation, associated with a higher degree of environmental aridity and higher annual average temperatures (Gómez-Mestre, 2014). The viper *V. latastei* is a species typical of humid, sub-humid and semi-arid Mediterranean climates with a preference for plains and warm areas, rocky areas with scattered vegetation cover, as well as forest glades (Brito, 2011). *P. waltl* is a fully thermophilic newt, and is currently the only salamander present in the eastern Iberian Mediterranean area, where it occupies the thermo-Mediterranean, meso-Mediterranean and supra-Mediterranean bioclimates (Montori et al., 1997, 2002).

Also characteristic of the fossil record of this region is the presence of *T. hermanni*, which during the Late Pleistocene presents a continuous record from the previous interglacial (MIS 5e) until the period before the Last Glacial Maximum (MIS 2), confirming the prehistoric distribution of this land tortoise in the Iberian inland and along the Atlantic coast. These are regions where it is now extinct (Morales and Sanchis, 2009) and *T. hermanni* is currently associated with limited coastal areas with a Mediterranean climate in the northern half of the Iberian Mediterranean coast, although in

the east of its Mediterranean distribution in Italy and the Balkans it also appears in sub-Mediterranean climates, living in open environments, such as glades in wooded areas, shrublands or dune grasslands (Bertolero, 2010). Temperatures mark the viability of *T. hermanni* embryos, which die at temperatures below 25 °C or above 35 °C (Eendebak, 1995), possibly serving to establish one of its climatic barriers, based on the maximum/minimum temperatures of the months between the egg laying and eclosion from mid-May to early October (Bertolero, 2010).

The association of species typical of the Atlantic Iberian area such as *T. pygmaeus*, *C. striatus* or the genus *Lissotriton* in the Pleistocene levels of Gorham's Cave (MIS 3–1, 32,500–10,800 B.P.), along with predominantly thermo-Mediterranean faunal and botanical records, suggest the existence of a southern glacial *refugium* for the herpetofaunal species of the western Iberian Peninsula during the most critical climatic phases of the Late Pleistocene, within their parameters of habitability but outside their current distribution areas (Blain et al., 2013). A clear example of this approach is the current absence of the genus *Lissotriton* in the Iberian part of the Strait of Gibraltar, the *L. boscai* populations of the Doñana National Park being the closest to Gorham's Cave, which is located more than 120 km away (Díaz-Paniagua, 2002). This raises the possibility that there was first an expansion of its distribution towards the south during the last glacial phase and subsequently a retraction of the populations towards the north during the Holocene.

The continued presence of the gecko *T. mauritanica* is significant from the previous interglacial (MIS 5), with the sequence from Vanguard's Cave (Gleed-Owen, 2001; Gleed-Owen and Price, 2012), to the present, with records ranging from MIS 3 to MIS 1 in the sequences from Boquete de Zafarraya and Gorham's Cave (Barroso and Bailon, 2003; Barroso et al., 2003; Blain et al., 2013). This fossil record confirms its indigenous Iberian character from prior to the Holocene and contradicts the theory of its introduction by humans in recent times (Mayol, 1985; Harris et al., 2004a). This also coincides with the genetic diversity of the *T. mauritanica* populations observed in central and southeast Iberia, with three different lineages identified (Harris et al., 2004b; Perera and Harris, 2008), the central populations presenting an old mitochondrial lineage that refutes the theory of its recent introduction and corroborates its autochthony, at least in the case of these central populations. In fact, the genetic distance among the Iberian populations of *T. mauritanica* is so high that it could possibly be ascribed to two different species, the native central species and a recently introduced species on the southern and eastern littoral (Rato et al., 2016). As yet, there is no description of osteological characters that would make it possible to differentiate between these two new species. The absence of *H. turcicus*, the other gecko currently present in the Iberian Peninsula, in the fossil record of the Late Pleistocene and the genetic homogeneity of its European populations, including the Iberian populations, raise the possibility of a very rapid dispersion from a point of origin in the eastern Mediterranean Sea in recent times and possibly caused by humans (Carranza and Arnold, 2006; Mateo et al., 2011). Later, it would have colonized the Iberian Peninsula from a bridgehead in North Africa, although the mitochondrial homogeneity of the European clade (clade A) may be due to selective sweep processes and not just a recent expansion (Rato et al., 2011). However, it should be noted that *H. turcicus* is a small gecko with a fragile osteology that may suffers problems of preservation in the fossil record.

The herpetofaunal assemblage of level A of Sala de las Chimeneas from Cueva de Maltravieso in Extremadura, dated to the final phase of the Last Glacial Maximum (between 19,500–18,700 cal. B.P. and 19,700–18,750 cal. B.P.) (Bañuls-Cardona et al., 2012), is composed of *B. spinosus*, *B. calamita*, *P. perezi*, *T. lepidus*, (cf.) *N. maura*, *C. girondica* and *V. latastei*, an association that shows the survival of a thermophilic Mediterranean herpetofauna within the Iberian Peninsula even in the most critical glacial times of the latest Pleistocene. The herpetofaunal fossil record of central and southern areas is rich if compared with the other two regions analyzed, even though the central area is lower in the number of species than the Andalusian and Portuguese regions. This is the case with the MIS 1 sequence from Peña de Estebanvela prior to the Younger Dryas, with the concurrence of the anurans *Alytes* sp. and *B. calamita* in level VI (14,450 ± 80 B.P. & 14,200 ± 50 B.P.) or only *B. calamita* in levels IV, III and II during the Younger Dryas (12,530 ± 60 B.P. to 11,400 ± 120 B.P.) (Sanchiz and Barbadillo, 2007; Sanchiz and Bailon, 2013). However, in level I of Estebanvela de Peña, dated at between 11,330 ± 50 cal. B.P. and 10,640 ± 60 cal. B.P., there appears the association of *B. calamita*, *T. lepidus*, *M. monspessulanus*, *Z. scalaris*, (cf.) *Coronella* sp. and *V. latastei*, similar to that documented in level A of Sala de las Chimeneas. In this case it is an assemblage of a markedly Mediterranean herpetofauna occurring at a level assigned to the cold climatic phase of the Younger Dryas. Both cases, level A of Sala de las Chimeneas and level I of Peña de Estebanvela, seem to indicate a climate scenario that is less aggressive than might have at first been thought for the thermophilic and/or typical Mediterranean species of the Iberian inland during the latest Pleistocene. Another thermophilic assemblage dating to MIS 2 is that documented in level IV of Cueva Higueral de Valleja (18,300 ± 4800 B.P. and 15,500 ± 3700 B.P.), in the region of Cadiz, where appear in concurrence *B. calamita*, *T. mauritanica*, *N. maura*, *M. monspessulanus*, and *Z. scalaris* (Jennings et al., 2009).

In the eastern Mediterranean strip of the studied area, the herpetofaunal fossil record of the Valencian Country is characterized by the scarcity of publications of prehistoric assemblages and the high degree of mono-specific citations in the literature, which is basically monopolized during the Late Pleistocene by *T. hermanni* and *Testudo* sp. (Morales and Sanchis, 2009; Sanchis et al., 2015), a species easily identifiable in the zooarchaeological record by contrast with the non-chelonian herpetofauna. Thus, in the Late Pleistocene of the Valencian Country, this typically Mediterranean turtle is documented in the MIS 5e levels of Cova de Bolomor (Fernández Peris, 2007; Blasco, 2008), the Mousterian levels of Cova Negra of Xàtiva (Pérez Ripoll, 1977), in Abrigo de la Quebrada (Sanchis et al., 2013), Abric del Salt (Morales and Sanchis, 2009; Pérez Luís, 2014), Abric del Pastor (Galván et al., 2008; Sanchis et al., 2015), San Luís of Buñol (Fernandez Peris and Martínez Valle, 1989) and the Pleistocene sequence of Cova Canet of Aielo de Malferit (Morales and Sanchis, 2009). Further, the presence of indeterminate chelonians is recorded in the Cova de Dalt Tossal de la Font of Vilafamés, possibly associated with an accumulation caused by a group of hyenas (Saladié et al., 2010). In addition to *T. hermanni*, the presence of the toad *B. spinosus* (Luis Perez, 2014) has also been identified in level X of Abric del Salt. In the Valencian Pleistocene record, there is evidence of the human consumption (by *H. neanderthalensis*) of turtles in Bolomor, Abrigo de la Quebrada and Abric del Pastor (Blasco, 2008; Galván et al., 2008; Sanchis et al., 2013, 2015).

As regards the Valencian Holocene, citations of the presence of *Testudo* sp. from the Chalcolithic archaeological site of Ereta del Pedregal (Pérez Ripoll, 1990) have recently been assigned to *M. leprosa* and Emydidae/Geoemydidae indet. (Morales and Sanchis, 2009). An individual belonging to *M. leprosa* has also been identified in the Neolithic levels of Cova de l'Or (Pérez Ripoll, pers. com.). In Lloma de Betxí, dated to between 2100 cal. B.C.E. and 1600 cal. B.C.E. and assigned to the Valencian Bronze Culture (De Pedro, 2004), *B. spinosus*, *M. leprosa*, *T. lepidus* and *Elaphe* sp. have been identified in concurrence (Tormo and De Pedro, 2013); this latter taxon may be *Z. scalaris*, the only species from the complex of

the genus *Elaphe* sensu lato that is present in the Valencian Country, which also includes *Z. longissimus* (Pleguezuelos, 2009; Rubio and Gosá, 2010). *M. leprosa* is also documented in phase III of the Bronze Age from Pic dels Corbs, dated to between 1400/1350 cal. B.C.E. and 1100/1050 cal. B.C.E. (Barrachina and Sanchis, 2008).

The prehistoric herpetofauna known from the final Late Pleistocene and the Late Holocene of the Valencian Country is quite poor when compared with the rest of the Iberian Peninsula, both in the number of sites with a published record and in the number of taxa identified, by contrast with the relatively good knowledge of its archaeological record. Assemblages such as those from Lloma de Betxí with *B. spinosus*, *M. leprosa*, *T. lepidus* and *Elaphe* sp. (= *Z. scalaris*?) and the combination of *T. hermanni* and *B. spinosus* from Abric del Salt represent exceptions within the Valencian herpetofaunal fossil record.

The Portuguese Atlantic region also suffers from a scarcity of sites with a published prehistoric herpetofauna for the period studied. However, by contrast with the Valencia Country, two Portuguese sites have assemblages with a significant number of species: Gruta da Figueira Brava (MIS 3) and Guia de Albufeira (Pleistocene phase of MIS 1) (Crespo et al., 2000; Crespo, 2002). In both herpetofaunal associations there are typically thermophilic species such as *B. cinereus-mariae*, *T. lepidus* and *P. cultripes*, along with other species such as *P. waltl* and *A. erythrurus*, which also have a fossil record in the Andalusian Late Pleistocene. In addition, there are chelonian citations from Gruta Nova da Columbeira (*T. hermanni* and Emydidae indet., MIS 3), Gruta do Caldeirão (*T. hermanni* and *M. leprosa*, MIS 2) and Gruta do Escoural (*T. hermanni*, MIS 2), as well as the turtle assemblage from Gruta da Figueira Brava (*T. hermanni* and *E. orbicularis*, MIS 3) (Crespo et al., 2000; Crespo, 2002; Morales and Sanchis, 2009; Nabais, 2012).

Apart from its appearance in Gruta do Caldeirão, *M. leprosa* does not have a known record for MIS 3 and 2 in the Iberian Peninsula. However, the number of citations of this turtle increases greatly during the Holocene, above all from the Neolithic onwards (Jiménez Fuentes, 1986; Budó et al., 2005; Félix et al., 2006; Barrachina and Sanchis, 2008; Morales and Sanchis, 2009; Tormo and De Pedro, 2013). In contrast, the other freshwater Iberian turtle, *E. orbicularis*, has a greater number of Late Pleistocene records, namely in the Mousterian sequences from Figueira Brava and Gruta Nova da Columbeira (Emydidae indet.), level IV of Gorham's Cave (Emydidae indet.) and level NM14 of Cueva de Nerja (Jiménez Fuentes, 1986; Gómez and Jiménez Fuentes, 1998; Crespo, 2002; Blain et al., 2013). Genetic studies of current Maghrebian and Iberian populations of *M. leprosa* suggest that it recently colonized the Iberian Peninsula from populations to the north of the Atlas Mountains or even from a bridgehead at the southern tip of the Iberian Peninsula itself, because the Strait of Gibraltar was possibly not an impermeable barrier to genetic exchange between *trans*-Mediterranean populations of freshwater turtles (Fritz et al., 2006; Velo-Antón and Pinya, 2015a). The genetic scenario amongst the Iberian populations of *E. orbicularis* is much more diverse, with four different clades identified, at least one of them endemic. Of the remaining three, one appears on both sides of the Strait of Gibraltar and the other two clades have eastern and *trans*-Pyrenean origins and appear in the northern half of the Iberian Mediterranean coast and the Ebro Valley (Velo-Antón et al., 2015; Velo-Antón and Pinya, 2015b). Therefore, the data provided by genetic studies are consistent with the scenario presented by the fossil record, with the possible extinction of *M. leprosa* from most (or even all) of the Iberian Peninsula, while *E. orbicularis* maintained populations in Iberia during the Late Quaternary, being a much less thermophilic species than *M. leprosa*. The onset of the current interglacial would have allowed *M. leprosa* to recolonize the Iberian Peninsula from the Straits of Gibraltar, as well as permitting the arrival of new populations of *E. orbicularis* from the Maghreb and *trans*-Pyrenean Europe.

As regards species with no fossil record between MIS 3 and MIS 1, there are citations of *Alytes* sp. and *Lissotriton* sp. from Gorham's Cave (Blain et al., 2013) and of *Alytes* sp. from Peña de Estebanvela (Sanchiz and Barbadillo, 2007; Sanchiz and Bailon, 2013), which by their geographical distribution could correspond to *A. cisternasii*/*dickhilleni* and *L. boscai* and to *A. obstetricans*/*cisternasii*, respectively. *H. meridionalis* could have its last Pleistocene fossil record in the Mousterian levels from Vanguard's Cave of Gibraltar, dated to MIS 5 (Gleed-Owen, 2001; Gleed-Owen and Price, 2012), therefore being absent from the rest of the Pleistocene and from the sites hitherto known for the Holocene, when it could have crossed the Strait of Gibraltar to colonize southwest Iberia (Tejedo and Reques, 2002).

Finally, another species of North African origin, *C. chamaeleon*, has a single zooarchaeological record in the Bronze Age levels of Cueva de la Victoria of Málaga (Talavera and Sanchiz, 1983), being absent throughout the rest of the fossil record of the Iberian Quaternary. This has not been included in the regional data matrix because it is a mono-specific citation. The statistical methods applied to the regional data matrix suggest a scenario of great stability in the herpetofaunal composition of the center and south of the Iberian Peninsula, with little observable change by chronological level. Climatic and environmental changes linked both to the last glacial phase and the subsequent interglacial onset seem not to have had large impacts on the herpetofaunal composition of this area. The detected biogeographic changes are the contraction of the southern boundary in the distribution of some taxa (e.g., genus *Alytes* and L. *boscai* in the Gibraltar region), the possible recolonization by *M. leprosa* from the Maghreb, and the entry of new species such as *H. meridionalis* and *C. chamaeleon*, also from North Africa. In the future, data on the prehistoric herpetofauna of central and southern Iberia are expected to increase from the ongoing study of significant sites such as Pinilla del Valle and new campaigns in the caves of Gibraltar, Castillejo del Bonete and Maltravieso.

4.4. General discussion

The apparent absence of some species in the fossil record, especially those of smaller size, may be due to multiple factors of destruction and selection, processes also observed in the bias towards specific skeletal elements (Esteban and Sanchiz, 1985). At an ecological level, the lack of specialized predators of particular species of amphibians and reptiles reduces the taphonomic bias generated by them to criteria such as the size of prey or individual visibility at hunting time (Blain, 2009), which may generally affect species of smaller sizes.

One of the most difficult groups when it comes to species-level taxonomic identification is Lacertidae, especially the species of small size, which includes the genera *Podarcis* and *Psammodromus*. *Podarcis* is a lizard genus that currently shows a large specific diversity, manifest in its phylogenetic complexity in the Iberian Peninsula (Kaliontzopoulou et al., 2011). Within this genus, *P. hispanica* (sensu lato) is a paraphyletic taxon that groups most of the rupicolous Iberian lizards, with a distribution that covers most of the Iberian Peninsula up to the isotherm of 14 °C and with significant insolation requirements (Sá-Sousa and Pérez-Mellado, 2002). With the advance of molecular investigations into this taxon, at least six news species have been separated and described, *Podarcis carbonelli*, *P. bocagei*, *P. vaucheri*, *P. liolepis*, *P. guadarramae* and *P. virescens* (Harris and Sá-Sousa, 2001, 2002; Harris et al., 2002; Pinho et al., 2003, 2006, 2007b, 2008, 2009; Renoult et al., 2010; Geniez et al., 2014). Thus, *P. hispanica* sensu stricto is restricted to the Mediterranean eastern area and southeastern

Iberia (Geniez et al., 2007). Genetic analyses show that this varied and extensive speciation was the result of a rapid process of allopatric diversification that occurred in a short time period, with different lineages that appeared in relatively small geographical areas. This scenario is associated with the existence of "*refugia within glacial refugia*" in the Iberian Peninsula (Pinho et al., 2007a), a vicarious regionalization of the Iberian distribution of these species in accordance with the different climatic conditions and geographical barriers.

With a currently poor fossil record that precludes an archaeopaleontological approach because of the lack of criteria for taxonomic identification based on the skeletal remains of these new, recently described species, the correlation between the current distribution of the *P. hispanica* complex, the theoretical expansions during the postglacial period and the geographical disposition of their glacial *refugia* can be used to locate those regions that kept optimal climatic conditions for these relatively thermophilic lizards through the different Pleistocene glaciations. Furthermore, a better genetic understanding of the Iberian populations of *P. muralis*, a different species of lizard that is not part of the *P. hispanica* complex, as well as the determination of better osteological characters that may lead to its taxonomic identification in the fossil record, would permit a comparative scenario between these two taxa, since *P. muralis* is a lizard that is much more resistant to Euro-Siberian conditions, which a priori would allow greater adaptability and a wider distribution during the Pleistocene cold phases.

Currently, *P. muralis* occupies the Iberian Euro-Siberian fringe, but also presents two southern relict populations limited to the Central System and the Iberian System mountain ranges that are isolated from the northern populations (Pérez-Mellado, 2002; Diego-Rasilla, 2009), suggesting a greater distribution in the past. At the moment, the data available from its Iberian populations suggest the existence of two endemic clades, clade 2 in the Cantabrian Mountains and clade 3 in the Central System and the Iberian System, plus a third clade in the Pyrenees which is also distributed in western France (clade 1). Furthermore, it has been found that the discontinuity in the distribution of its Iberian populations does not correspond to a genetic discontinuity, so the fragmentation process is due to recent dynamics (Salvi et al., 2013), which can be associated with the effects of climate change in the current interglacial. Two other lizards linked to Euro-Siberian climates and/or to Alpine environments, which show phylogeographies that suggest a long evolutionary history in the Iberian Peninsula, are *Z. vivipara* and the genus *Iberolacerta* (Crochet et al., 2004; Milá et al., 2013) although these have not been identified in the fossil record to date.

Another Iberian lizard, *L. schreiberi*, has four distinct lineages, two coastal clades located on the northern and southern Atlantic littoral, and two inland clades present in the Central System and in the populations of the southern mountain ranges, respectively. These inland clades and the southern coastal population are associated with possible glacial *refugia* for this lizard, the northern coastal lineage being the only one that presents an expansive distribution during the postglacial (Paulo et al., 2001, 2002a). By contrast, processes of genetic divergence reflecting east-west allopatry have been described for Iberian populations of *P. waltl*, *P. algirus*, *A. erythrurus* and *D. galganoi*, associated with the existence of two favorable climatic areas serving the function of a glacial *refugium* in southeastern and southwestern Iberia (Schmitt, 2007). In contexts beyond the reach of "classic" zooarchaeological studies due to the limitations of a purely osteological taxonomy, molecular studies provide an open window onto the distribution of species in the past and their paleoclimatic and paleoenvironmental implications, always bearing in mind the difficulty of reading and dating the genetic isolation of herpetofaunal populations.

The herpetofaunal fossil record of the Iberian latest Quaternary is very rich and varied in comparison with contemporaneous associations documented in Central Europe, which has associations of *S. salamandra*, *Triturus cristatus*, *Triturus vulgaris*, *Bufo bufo*, *Bombina bombina*, *Hyla arborea*, *Pelobates fuscus*, *R. dalmatina*, *R. temporaria*, *Pelophylax ridibunda*, *E. orbicularis*, *A. fragilis*, *Lacerta viridis*, *N. natrix* and *Z. longissimus* during the interglacial optimum, joined in the colder stages of the interglacial by the species *B. calamita*, *Bufotes viridis*, *Rana arvalis*, *L. agilis* and *C. austriaca*, together with *T. vulgaris*, *B. bufo*, *H. arborea*, *P. fuscus*, *R. temporaria*, *P. ridibunda*, *A. fragilis* and *N. natrix*. This herpetofaunal diversity is reduced drastically with the onset of the glacial phase, with associations of *B. viridis*, *R. temporaria*, *Z. vivipara* and *Vipera berus* reported, and finally only the frog *R. temporaria* in the glacial maximum (Böhme, 1996, 2010, 2000).

The Iberian scenario shows the continued presence of thermophilic species in the center and south of the Iberian Peninsula and their survival in the most critical moment of the last glacial phase (Fig. 5), the Last Glacial Maximum, with a typical Mediterranean assemblage of *B. spinosus*, *B. calamita*, *P. perezi*, *T. lepidus*, (cf.) *N. maura*, *C. girondica* and *V. latastei* in level A of Sala de las Chimeneas from Cueva de Maltravieso (Bañuls-Cardona et al., 2012). Another pleniglacial herpetofaunal assemblage that is richer than the Central European scenario has also been cited in northern Iberia, with the association of *A. obstetricans*, *B. spinosus*, *B. calamita*, *R. temporaria*, Lacertidae indet. and *Vipera* sp. in levels 6 to 3 of El Portalón de Atapuerca, also dating from the Last Glacial Maximum (López-García et al., 2010b).

Another possible comparison is with the rodent fossil record of the Iberian latest Quaternary, which is characterized by the appearance of most current species, such as *Chionomys nivalis* and *Iberomys cabrerae*, the extinction of *Pliomys lenki*, *Iberomys brecciensis* and *Allocricetus bursae* as well as the disappearance of the Iberian populations of *Microtus oeconomus*, *Microtus gregalis*, *Castor fiber* and *Hystrix brachyura* (Sesé and Sevilla, 1996; López-García, 2008). The emergence of new rodents such as *Mus spretus*, *Mus musculus*, *Micromys minutus*, *Rattus rattus* and *Rattus norvergicus* occurred throughout the Holocene, and these are species related to humans by commensalism (Sesé and Sevilla, 1996). By comparison, among reptiles and amphibians the scenario is more static and limited to the glacial restriction of thermophilic and/or Mediterranean taxa to central and southern Iberia, with the subsequent colonization by some of these species of the northern Iberian regions taking advantage of the postglacial climate improvement, but without the total extinction of any species identified in the latest Pleistocene record (Fig. 5). The appearance in the Holocene of species without an Iberian fossil record in the latest Pleistocene, such as the anuran *H. meridionalis*, the tortoise *Testudo graeca*, the gecko *H. turcicus* and the chameleon *C. chamaeleon*, has been linked to human introductions; all of them have clear phylogenetic relationships with populations located on the Maghrebian side of the Strait of Gibraltar (Pleguezuelos et al., 2008).

Z. longissimus is the only herpetofaunal case of a postglacial colonization from the other side of the Pyrenees currently verified both by the fossil record and by molecular studies (Musilová et al., 2010). However, this snake is unlikely to be the only taxon that used this route of colonization, as might have occurred with other reptiles with similar phylogeographies, such as *L. agilis* (Kalyabina et al., 2001) and *L. bilineata* (Brückner et al., 2001; Joger et al., 2001; Böhme et al., 2007), although there are no Iberian fossil records for these species. In the case of *H. viridiflavus*, which presents a postglacial fossil record in the Iberian Peninsula, the phylogeography of its Iberian populations is unknown (Nagy et al., 2002; Joger et al., 2007).

H. meridionalis, which is probably present in the Iberian Early

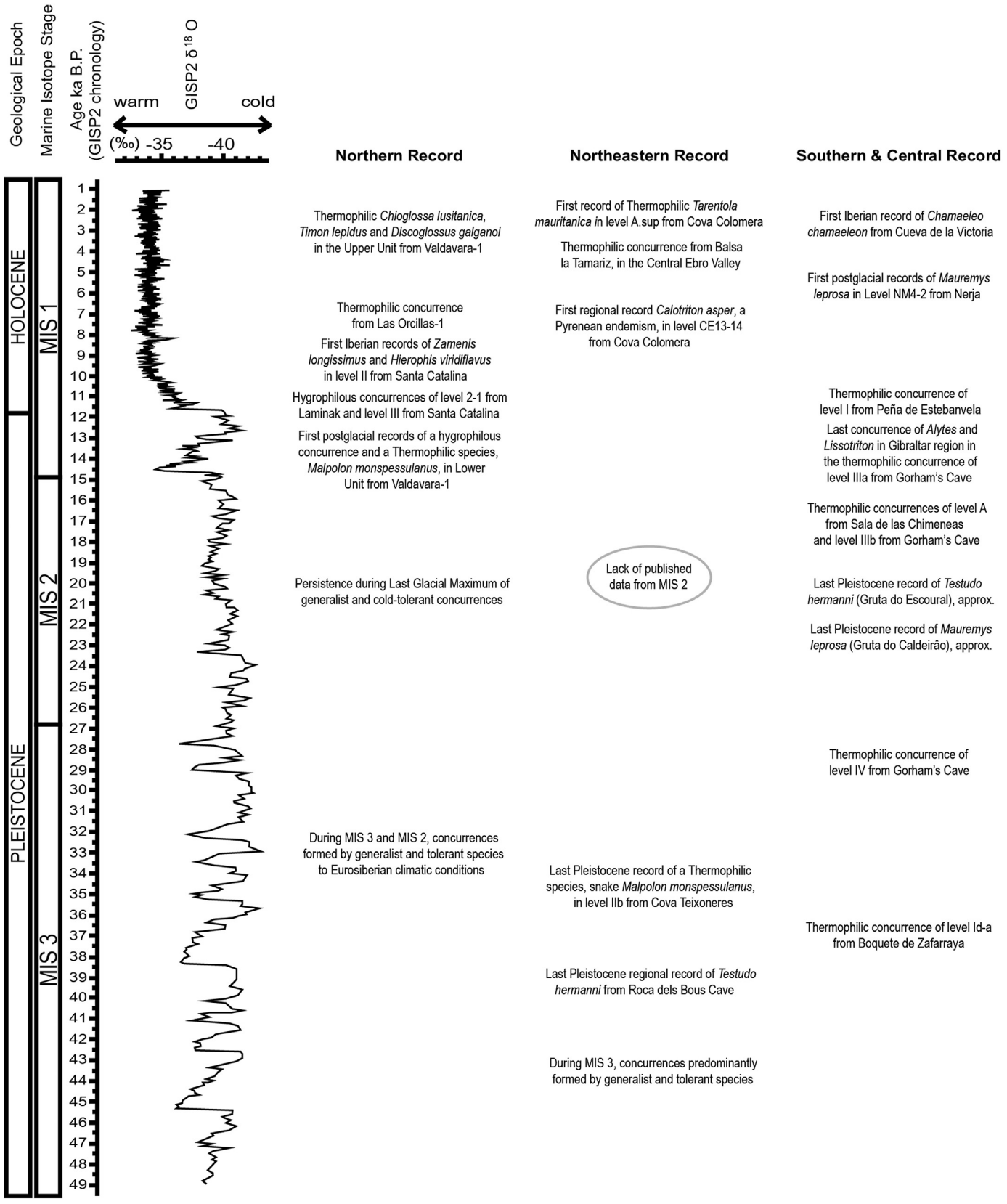
Geological Epoch
Marine Isotope Stage
Age ka B.P. (GISP2 chronology)
GISP2 δ18 O
warm
cold
(‰) -35
-40
HOLOCENE
PLEISTOCENE
MIS 1
MIS 2
MIS 3
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49
Northern Record
Thermophilic Chioglossa lusitanica, Timon lepidus and Discoglossus galganoi in the Upper Unit from Valdavara-1
Thermophilic concurrence from Las Orcillas-1
First Iberian records of Zamenis longissimus and Hierophis viridiflavus in level II from Santa Catalina
Hygrophilous concurrences of level 2-1 from Laminak and level III from Santa Catalina
First postglacial records of a hygrophilous concurrence and a Thermophilic species, Malpolon monspessulanus, in Lower Unit from Valdavara-1
Persistence during Last Glacial Maximum of generalist and cold-tolerant concurrences
During MIS 3 and MIS 2, concurrences formed by generalist and tolerant species to Eurosiberian climatic conditions
Northeastern Record
First record of Thermophilic Tarentola mauritanica in level A.sup from Cova Colomera
Thermophilic concurrence from Balsa la Tamariz, in the Central Ebro Valley
First regional record Calotriton asper, a Pyrenean endemism, in level CE13-14 from Cova Colomera
Lack of published data from MIS 2
Last Pleistocene record of a Thermophilic species, snake Malpolon monspessulanus, in level IIb from Cova Teixoneres
Last Pleistocene regional record of Testudo hermanni from Roca dels Bous Cave
During MIS 3, concurrences predominantly formed by generalist and tolerant species
Southern & Central Record
First Iberian record of Chamaeleo chamaeleon from Cueva de la Victoria
First postglacial records of Mauremys leprosa in Level NM4-2 from Nerja
Thermophilic concurrence of level I from Peña de Estebanvela
Last concurrence of Alytes and Lissotriton in Gibraltar region in the thermophilic concurrence of level IIIa from Gorham's Cave
Thermophilic concurrences of level A from Sala de las Chimeneas and level IIIb from Gorham's Cave
Last Pleistocene record of Testudo hermanni (Gruta do Escoural), approx.
Last Pleistocene record of Mauremys leprosa (Gruta do Caldeirão), approx.
Thermophilic concurrence of level IV from Gorham's Cave
Thermophilic concurrence of level Id-a from Boquete de Zafarraya

Fig. 5. Comparison of the main biogeographic changes and the most significant herpetofaunal assemblages in the Iberian Peninsula during the latest Quaternary with GISP2 oxygen isotope records (modified from Fletcher and Sánchez-Goñi, 2008).

Pleistocene (Blain, 2009; Agustí et al., 2010) but is apparently absent from the fossil record of the Late Pleistocene except for its appearance in the MIS 5b-a sequence of Vanguard's Cave (Gleed-Owen, 2001; Gleed-Owen and Price, 2011), has been reintroduced in recent times from two different areas of North Africa (Recuero et al., 2007). Something similar has been detected in the Iberian communities of *C. chamaeleon*, which were introduced from two populations in Atlantic and Mediterranean areas of the Maghreb (Paulo et al., 2002b). *H. turcicus* could have colonized the thermophilic Iberian littoral from populations in North Africa (Carranza and Arnold, 2006; Mateo et al., 2011; Rato et al., 2011). Meanwhile, the two Iberian populations of *T. graeca* share haplotypes with Maghreb populations, having reached the Iberian Peninsula either by human introduction or by natural rafting from northern Algeria in rather recent times, adding to the modern contributions of Moroccan individuals in the Doñana area (Álvarez et al., 2000; Fritz et al., 2009; Graciá et al., 2011, 2013, Graciá and Giménez, 2015). These are generally species of anthropophilic tendencies and, in the specific cases of *T. graeca* and *C. chamaeleon*, cultural linkages and magical-religious practices are known that could have led to their intentional introduction by humans (Pleguezuelos et al., 2008).

Returning to the north of the Iberian Peninsula, the reptiles *L. bilineata*, *Z. longissimus* and *H. viridiflavus* would have crossed the Pyrenees during the postglacial stage. These three species have reduced distributions in the Iberian Peninsula, basically focused on the two ends of the Pyrenees, the Basque-Cantabrian and Catalan areas (Santos et al., 2002a, 2002b; Barbadillo, 2002). In contrast to their situation in Iberia, they have an extensive and widespread distribution in Mediterranean environments of the Italian Peninsula and Sicily (Gosá and Rubio, 2013). Their restricted distribution in the Iberian Peninsula, despite their tolerance of fully Mediterranean climates and thermophilic environments, has been linked to competition with other Iberian species. *Z. scalaris* is considered the Iberian ecological equivalent of *Z. longissimus*, the two species excluding each other and appearing in sympatry only at the southern limit of the Pyrenean distribution of the latter species, but never in syntopy (Rubio and Gosá, 2010). Phenomena of allopatry by competition have been detected among *M. monspessulanus* and *H. viridiflavus* (Cortesogno, 1994; Naulleau, 1997), it being the competitive exclusion with *M. monspessulanus* that determines the southern boundary of the Iberian distribution of *H. viridiflavus* (Santos et al., 2010). For L. *bilineata*, the existence of competitive exclusion with *L. schreiberi* and *T. lepidus* has also been suggested, though more data are needed to confirm this (Delibes and Salvador, 1986; Gosá and Rubio, 2013). *R. dalmatina*, which has a possible Pleistocene record in Erralla (Esteban and Sanchiz, 1985), could be included in the same category as the above-mentioned species on account of its reduced Iberian distribution range (Gosá, 2002), bounded to the south of the Basque Country and northern Navarra, in contrast to its expansion in Italy and the Balkans. This could be due to competitive exclusion processes with *R. temporaria* (Riis, 1997).

In projections of the current area of potential habitability for these four species in the Iberian Peninsula (Araújo et al., 2011), the potential viability of *R. dalmatina* is proposed along the Cantabrian fringe, in the northern half of Portugal and the western and central Pyrenees, where the potential area of *R. dalmatina* habitability overlaps with the distribution of *R. temporaria*. The same area of potential habitability is attributed to *L. bilineata*, where one of its possible Iberian ecological opponents is also located, the northwestern Iberian endemism L. *schreiberi*. For this latter lizard an area of potential habitability is proposed that ranges from the Basque Country to Catalonia through the Pyrenees and the southern pre-Pyrenean valleys, the two ends of the Pyrenees being occupied by *L. bilineata*. This reinforces the hypothesis of competitive exclusion between the two species of the genus *Lacerta*. By contrast, *Z. longissimus* and *H. viridiflavus*, which share roughly the same potential habitability area as *L. bilineata* and *R. dalmatina*, only come into direct conflict with *Z. scalaris* and *M. monspessulanus* in the Atlantic fringe that runs from the southern half of Galicia to the river Tagus.

However, it should be noted that Araújo et al. (2011) only include climate data for the Iberian populations in making their projections of potential distribution. Hence, it is possible that the potential habitability of *L. bilineata*, *Z. longissimus* and *H. viridiflavus* in Iberian Mediterranean regions has been underestimated due to the apparent Euro-Siberian affinities of these species in Iberia, when in fact they are species capable of living in much warmer areas in the other southern European peninsulas. For this reason, the hypothesis cannot be ruled out that the southern limits of their distributions are due to direct competition with *T. lepidus*, *Z. scalaris* and *M. monspessulanus*, respectively.

5. Conclusions and future prospects

In all 58 Iberian archaeo-paleontological sites with a herpetofaunal presence from the latest Pleistocene to the Late Holocene a total of 47 different taxa have been identified at generic and specific level. These are grouped taxonomically into eight urodelans: *P. waltl*, *S. salamandra*, *T. pygmaeus*, *T. marmoratus*, *I. alpestris*, *C. asper*, *C. lusitanica* and *L. helveticus*; 12 anurans: *A. obstetricans*, *A. cisternasii*, *D. galganoi*, *P. cultripes*, *B. spinosus*, *B. calamita*, *R. temporaria*, *R. dalmatina*, *R. iberica*, *P. perezi*, *P. punctatus* and genus *Hyla*; three chelonians: *M. leprosa*, *E. orbicularis* and *T. hermanni*; one amphisbaenian: *B. cinereus-mariae*; one iguanian: *C. chamaeleon*; one gecko: *T. mauritanica*; one anguimorph: *A. fragilis*; two skinks: *C. bedriagai* and *C. striatus*; five lizards: *A. erythrurus*, *P. algirus*, *T. lepidus* and genera *Lacerta* and *Podarcis*; and 13 snakes: *N. maura*, *N. natrix* sensu lato, *C. austriaca*, *C. girondica*, *H. hippocrepis*, *Z. longissimus*, *Z. scalaris*, *H. viridiflavus*, *M. brevis*, *M. monspessulanus*, *V. aspis*, *V. seoanei* and *V. latastei*.

The fossil herpetofaunal assemblages allow us to establish two major biotic regions during the latest Pleistocene, albeit with ill-defined limits because of the current lack of a continuum of paleo-archaeological sites with a herpetological record between the two groups. The first biotic region is formed by the center and south of the Iberian Peninsula, with *B. calamita*, *B. spinosus*, *T. lepidus*, *Z. scalaris* and, to a lesser extent, *P. waltl*, *P. cultripes*, *T. hermanni*, *M. monspessulanus* and *V. latastei* as the most representative species of the herpetofaunal record. The second major biotic region comprises the Atlantic-Cantabrian facade and northeastern Iberia and is characterized by the association of *R. temporaria* and *A. fragilis* as the dominant species of the prehistoric sequences, although in the northern area they are accompanied by *B. spinosus*, *B. calamita* and the genera *Alytes* and *Vipera* as the most representative taxa, while in the northeastern Iberian record they are accompanied by *A. obstetricans*, *B. calamita*, *B. spinosus*, *P. punctatus* and *C. girondica* as the dominant species.

The paleoclimatic implications of these large associations indicate the maintenance of typically dry Mediterranean conditions in the central and southern regions, while the northern and northeastern areas present a generally mild and humid climatic regime dominated by wooded spaces and wet meadows. However, this scenario may be affected by the possible bias of a record with widely scattered sites in the south and center of the Iberian Peninsula, and the absence of published herpetofaunal assemblages for MIS 2 of the northeastern area. New discoveries and publications, which may fill the gaps in the different regional records, will confirm or challenge these observations.

The main biogeographic changes occur after the beginning of the postglacial phase, with the resulting climate improvement that produced the expansion of the thermophilic species towards the north of the Iberian Peninsula, possibly taking advantage of the existence of natural corridors such as the Ebro Valley or the Atlantic coast. In parallel, new Italian species entered via the Pyrenean margins having passed through southern France; their expansions may have been halted in the north by the contemporaneous colonization of Iberian Mediterranean species from the south. The introduction of various Maghrebian species, possibly caused by humans and dated by genetic studies to relatively recent times, represents the most recent processes of emergence and expansion of new amphibians and reptiles in the Iberian Peninsula during the Middle-Late Holocene.

New prospects are also opened up for increasing our knowledge of the herpetofauna reported in archaeological sites from cultural phases that saw the rise of a sedentary human lifestyle and the spread of agriculture and husbandry, i.e., from the Neolithic period. Increased attention to the archaeo-herpetological record of this chrono-cultural phase, in which the human impact and pressure on the landscape increased, will enable us to see how species of amphibians and reptiles adapt to anthropic changes in the environments near human settlements and to the newly generated ecological niches, even within the settlements themselves, ascertaining whether such changes help or impede the appearance of these species in the zooarchaeological record. Also of special interest are future studies of the records from those periods that saw an intensification of cultural and commercial contacts with other Mediterranean regions, from the Neolithic to the arrival of Phoenician and Greek settlers and traders in the Iron Age or the establishment of the Roman dominion in the Iberian Peninsula. These movements of people, ships and goods have been linked with the possible introduction, intentional or not, of herpetofauna from other regions, a phenomenon that still occurs today though on a global level, bringing the problem of alien and invasive species that enter the natural environment, exemplified by the case of *Trachemys scripta* in present-day Iberia.

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Appendices A, B & C. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.quascirev.2017.06.010.

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